UNIVERSITÉ DU QUÉBEC EN ABITIBI-TEMISCAMINGUE

ÉVALUATION DE LA PLASTICITÉ DES TRAITS DU BOULEAU À PAPIER DANS UNE EXPÉRIENCE EN JARDINS COMMUNS

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN ÉCOLOGIE

PAR

JENNA M. RABLEY

SEPTEMBRE 2021

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Annie DesRochers for her continued support over the course of my masters degree. Your insightful guidance and encouragement has helped me grow as a reasearcher. I believe my experience working with you has helped me prepare for a successful career in the environemental sector. Further, I appreciate the immense time you have dedicated to my project. Special thanks to Dr. Jian Wang and Dr. Philippe Marchand for answering questions related to statistical analysis and for providing helpful feedback.

Thank you to Philippe Duval, Michel Guimond and Eva Thévenin for your help collecting samples and taking measurements in the field. In addition, I would like to thank my student colleagues at the Amos campus including Léa Darquié, Dìary Gaspard, Ablo Hounzandji, Nada Aloui, Myriam Pilliet, Abhishek Tripathi, Brahim Maylal, Elyasse ElMrabet and Marwa Kraouaia for their consistant encouragements.

Huge thanks to my friends and family for supporting me in my endevours and providing endless motivation. To my mom, thanks for taking an active interest in my research and always providing emotional support. To my sister, Ali, thank you for your words of encouragement and comedic relief. To one of my dearest friends, Katehrine Standen, thank you for always being one of my greatest cheerleaders and soundboard. I appreciate your wisdom and friendship immensely. Lastly, Vanessa Riddell, Matthew Williams and Nathan Williams, thank you for being the best friends I could ask for – your endless praise, motivation and welcomed breaks for light hearted chats and fishing adventures were much appreciated.

FOREWORD

This manuscript has been divided into three chapters. The first chapter includes the general introduction, which provides a synthesis of academic literature in addition to the context and objectives of our research study. Chapter two is presented as a scientific article by the authors of “Jenna Rabley, Philippe Duval and Annie DesRochers”. The plantations used in the study were designed and planted by co-authors, Francine Tremblay and Philippe Duval. I am primarily responsible for study design, data collection, analysis and writing, however, co-authors Annie DesRochers and Francine Tremblay contributed to the project conception. Additionally, co-author and director, Annie Desrochers assisted in the interpretation of results and critically reviewed the content of the article. The final chapter contains the general conclusion, which includes a synopsis of the study, the implications of our findings and research perspectives.

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LIST OF ABBREVIATIONS AND SYMBOLS

AIPL	Wood production intensification area
SLA	Specific leaf area
$\delta^{13}C$	Ratio of stable isotopes ^{13}C : ^{12}C in parts per thousand
RD	Rapide-Danseur
DH	Duhamel-Ouest
LM	La Motte
MB	Montbeillard
SN	Senneterre
N_{leaf}	Leaf nitrogen content
ATP	Adenosine triphosphate
ADP	Adenosine diphosphate
N	Nitrogen
P	Phosphorous
K	Potassium
Mg	Magnesium

Ca	Calcium
Fe	Iron
WUE	Water use efficiency
CO_2	Carbon dioxide
^{12}C	Carbon-12 isotope
^{13}C	Carbon-13 isotope
DBH	Diameter at breast height
HNO_3	Nitric acid
HCL	Hydrochloric acid
P_N	Total photosynthetic rate
MAT	Mean annual temperature
MTWP	Maximum temperature during warmest month
MTCP	Minimum temperature during the coldest month
ATR	The annual temperature range (difference between the maximum temperature of the warmest period and minimum temperature of the coldest period)
DD>5°C	Number of growing degree days above 5ºC
MSP	Mean summer precipitation
MAP	Mean annual precipitation

PCA	Principal component analysis
PC	Principal component
NSERC	Natural Sciences and Engineering Research Council
CFS	Natural Resources Canada’s Canadian Forestry Service

RÉSUMÉ

Des études ont identifié une variation de plasticité dans les traits fonctionnels du bouleau à papier (*Betula papyrifera*) en raison de sa large distribution naturelle et de son grand degré de diversité génétique, permettant une adaptation locale compétitive et des caractéristiques physiologiques variables. Afin d'étudier les facteurs éco-physiologiques et environnementaux influençant l'établissement rapide, la croissance et la morphologie du bouleau à papier, nous avons conçu une expérience en jardin commun avec 8 provenances sur cinq sites distribués en latitude à travers l'Abitibi-Témiscamingue. La photosynthèse nette, la concentration en nutriments foliaires (N, K et P), la surface foliaire spécifique (SFS), la composition isotopique en carbone foliaire ($\delta^{13}C$), la croissance et les variables édaphiques ont été mesurées pour chaque provenance à chaque site. Les données climatiques ont été normalisées sur une tendance de 30 ans et utilisées pour déterminer l'effet de la translocation des provenances. Dix ans après la plantation, la taille moyenne et le taux de survie des provenances différaient entre les sites. Les stratégies d'acquisition de ressources des provenances ont montré de solides preuves de plasticité phénotypique, la productivité étant largement influencée par la qualité du site. Les sites productifs étaient caractérisés par une plus grande disponibilité en phosphore et des sols légèrement acides. De plus, la croissance a été négativement influencée par l'argile lourde et la compétition interspécifique. Les résultats de cette étude profiteront au secteur forestier canadien et augmenteront les marges bénéficiaires des propriétaires de boisés privés qui ont été ciblés pour l'établissement de plantations d’essences à croissance rapide et de haute qualité au Québec.

Mots clés : bouleau blanc, fonctions de transfert de provenance, jardin commun, isotopes de carbone, nutriments foliaires, plasticité phénotypique

CHAPTER I

GENERAL INTRODUCTION

1.1 Context

1.1.1 Forestry in Canada

The forestry industry is one of the most important resource sectors in Canada, generating 24.6 billion dollars of the country's gross domestic product in 2018 (Natural Resources Canada, 2018). Canadian forests are vital to the nation's economy, however, it is imperative to sustain these ecosystems to ensure health and productivity (Stedman et al., 2011). Research has shown that unsustainable forestry practices have led to forest degradation through the loss of biodiversity, soil erosion and increased atmospheric CO_2 concentrations (Lal, 2003). Destructive practices led to the development of the Canadian Council of Forest Ministers in 1985, who later enforced the sustainable forest management approach (Rousseau, 2003) pressuring provincial governments to improve forest exploitation regulations. In 2010, the Canadian government reported that forests, at a regional level, have shown a general trend in quality and structural decline indicating that further steps are required to ensure the forestry sector is operating as efficiently as possible while maintaining a competitive forest regime (Federal, Provincial and Territorial Governments of Canada, 2010).

Quebec forests currently face multiple sustainability pressures due to increased public demand to modify forestry practices, increase land area protected by the government

and sustain old growth forest development (Messier et al., 2003). A new law in the sustainable forest management act, proposed by the Quebec government, aims to address sustainability challenges by increasing the economic value of wood through the use of wood production intensification area (AIPL) (Laflèche and Cyr, 2013; Ministère des Forêts de la Faune et des Parcs, 2018). The AIPL aim to increase the wealth of public and private forest sectors by modifying forestry practices and integrating silvicultural techniques (Ministère des Forêts de la Faune et des Parcs, 2018). Sustainable practices have also been implemented through the use of tree breeding programs. Quebec has been using such methods for over 30 years and hybridization has been proven to increase stem quality, value and quantity (Huda et al., 2012; Rainville, 2003). The ability to select the most desirable trees from natural stands, breed them and improve the quality of their progenies could further increase the value of timber in AIPL zones (Huda et al., 2012). Today sustainable forest management has been implemented internationally and focusses on enforcing specific criteria and indicators that help measure and monitor sustainability by balancing ecological, social and economic needs (Duinker, 2001).

1.1.2 Economic importance of birch

Traditionally Quebec has invested time and resources into harvesting softwoods like *Picea* and *Pinus* genera due to the quality of their fiber (Natural Resources Canada, 2020). However, in recent years the industry has been shifting its focus to fast growing hardwood species within the *Larix* and *Populus* genera due to their rapid growth (Rainville, 2003). Similar to poplar and larix, *Betula papyrifera* Marsh (paper birch) is a medium sized but fast growing species (Safford et al., 1990). The calibre of its fiber has been recognized by the veneer industry and is used for pulp, furniture, wooden floors and specialty products (Rainville, 2003; Xue and Hu, 2009). Although similar in quality and quantity to that of its close relatives including *Betula lenta* L. and *Betula*

alleghaniensis B. (Wiedenbeck et al., 2004), paper birch is less expensive making it a suitable species for intensive management

Due to the wide range of its natural distribution (Figure 1.1) and large degree of genetic diversity, studies have identified plasticity variation within paper birch functional traits allowing for competitive local adaptation and varying physiological characteristics (de Villemereuil et al., 2016; Safford et al., 1990). Even with its known economic value, paper birch remains understudied in Canada. Only a few phenological studies and common garden experiments have been carried out in British Columbia (Benowicz et al., 2001; Hawkins and Dhar, 2012; Simpson et al., 1999) and little research has been done elsewhere in Canada creating knowledge gaps for this species. This is vastly different from other areas of the world that have documented the economic and environmental benefit of birch (Oikarinen, 1983; Viherä-Aarnio and Velling, 1999) as proven by Finland, where 16 percent of all trees planted are birch (Sevola, 2000).

The presence of paper birch within douglas-fir (*Pseudotsuga menziesii*) plantations has reduced mortality rates caused by *Armillaria ostoyae* root disease (Baleshta et al., 2005), increased nutrient cycling within plantation sites (Simard, 1996; Bockheim, 1991) and reduced the number of insect outbreaks compared to stands without paper birch (Simard, 1996). While studies have verified the economic and ecological potential of paper birch (Rainville, 2003; Baleshta et al., 2005; Simard, 1996) more information is required to better understand how to genetically improve this species to maximize economic gain in Quebec plantations.

1.2 Problem

Historically, there has been a lack of demand for the harvest of paper birch in Canada due to an underdeveloped market (Quigley and Babcock, 1969). However, in recent years North American industries have begun to recognize the value of birch fibre (Rainville, 2003; Godbout, 2002; Drouin et al., 2010). Currently, birch stands comprise

one of the highest merchantable volumes of timber in Quebec's hardwood forests (Natural Resources Canada, 2020) (Figure 1.1). Further, the genus is optimal for intensive management due to their large genetic pool and degree of trait variability (Safford et al., 1990). Thus, tree improvement programs can be used to improve the quality of paper birch for optimal growth.

Specifically, little research has been done in Quebec to investigate whether paper birch would express ecophysiological variation as a result of genetic or environmental influence in a common garden experiment. Based on vegetation composition, soil properties and climate, Quebec has been divided into ecological regions (Saucier et al., 2010). However, it still remains unclear to what extent environmental factors such as temperature and water availability influence growth differences amongst paper birch. Thus, translocating species to different bioclimatic zones could significantly impact timber production (Vitasse et al., 2009).

Located along the clay belt, Abitibi-Temiscamingue is heavily reliant on forestry and mining industries to support the region's economy (Gourd, 2007). However, the soil is largely made up of clayey lacustrine and loamy till deposits (Bergeron et al., 2007), potentially impacting the land capability to support productive plantations (Fox, 2000). Studies indicate root penetration and growth is dependent on the physical, chemical and biological makeup of soil (Jones, 1983). High concentrations of clay can lead to soil compaction and potentially impact root development (Jones, 1983). However, clay has a high water retention capacity and studies have documented that areas with high course fragmentation have provided favourable growing conditions for trees (Ravina and Magier, 1984). Our research aims to target these knowledge gaps within the literature to address how environmental factors and genetic variability influence the growth and function of transferred paper birch populations in Abitibi-Temiscamingue.

Figure 1.1 The forest composition and distribution of genera across Canada (Natural Resources Canada, 2020).

1.3 State of knowledge

1.3.1 Genetic control & environmental influence

Plants exhibit a large degree of ecophysiological and functional trait diversity as a way to cope with their heterogenous environments (Van Kleunen and Fischer, 2005). The evolution of phenotypic traits depends on phenotypic variation at biochemical and physiological levels within the developmental stages of a plant's ontogeny and their interaction with external environmental pressures (Price, 2003). In response to changing environmental conditions plants can alter their reaction norm due to the plastic nature of a trait (Pigliucci et al., 2006). Thus, phenotypic plasticity is when a single genotype is able to express multiple phenotypes (de Villemereuil et al., 2016) in

different environments (Joshi et al., 2001). In an unchanging environment, plant traits have an unexpressed plastic ability, however, the reaction norm remains unaltered (Pigliucci et al., 2006). When factors such as temperature, nutrients, water or light availability significantly alter normal environmental conditions, pre-existing reaction norms can shift and form a new phenotype so that the population can endure such changes (Pigliucci et al., 2006). However, the type and degree of plastic response varies between individual traits and environments (Gratani, 2014). Thus, some traits may be plastic in regards to light availability but not nutrient availability (Arntz and Delph, 2001).

If the new environmental conditions continue to persist the reaction to the norm may lose some of its plastic ability and become genetically fixed (Gratani, 2014). For example, plants from water limited environments have evolved to use water conserving traits, which can be seen across multiple plant lineages (Nicotra Davidson, 2010; Vendramini et al., 2002; Griffiths and Parry, 2002). Studies have also verified that plants will modify leaf traits such as specific leaf area (Gratani, 2014) and elongate internodes to avoid shaded areas and maximize access to light (Smith, 1982; Henry and Aarssen, 1997).

Traits under selection pressure increase a plant's ability to tolerate its environment and in turn increase overall fitness (Sultan, 1995). Researchers generally agree that natural selection acts on phenotypic plasticity, indicating that genetic control is a strong component (Grenier et al., 2016). However, given that the stresses present within the environment can induce plastic responses (Teklehaimanot et al., 1998; Ivancich et al., 2012; Zimmer et al., 2013) environmental impact on the evolution of given traits cannot be disregarded. Across various environments, members of the same species but of various populations may acquire different adaptive traits (Zimmer et al., 2013). The association between ecophysiological traits and resource uptake/utilization is well documented for species including spruce, pine (Beaulieu and Rainville, 2005;

Reinhardt et al., 2011) and poplar (Keller et al., 2011; Schreiber et al., 2011), however, paper birch remains understudied in Canada.

1.3.2 Ecophysiological & phenotypic variation

Plant species with widespread distribution may thrive as individual populations across various regions due to long term selection acting on functional traits (Gregor, 1946). Morphological and physiological adaptations reflect the stresses and pressures of an individual's local environment (Gregor, 1946; Bakhtiari et al., 2019). Thus, genotypes that have adapted to local conditions, create different ecotypes whereby the phenotypes expressed reflect high fitness (Bakhtiari et al., 2019). To determine whether the functional traits of a population are a result of phenotypic plasticity or local adaptation of an ecotype, transplantation experiments are frequently used (Hawkins and Dhar, 2012; Pletsers et al., 2015; Pyakurel and Wang, 2014; Reinhardtet et al., 2011).

Similar to phenotypic traits, but often associated with environmental control, morphological traits have shown to express genetic correlation (Waitt and Levin, 1998). It is clear that genotype plays a significant role in phenotypic expression, however, more research is required to document what degree of control the environment has in regards to physiological mechanisms of paper birch in Quebec.

Individuals of paper birch exhibit a high degree of phenotypic plasticity across Canada (Wang et al., 1998; Hawkins and Dhar, 2012; Pyakurel and Wang, 2014). Since adaption strategies vary across the landscape, studies have identified differences in water use efficiency and resource acquisition mechanisms (Perala and Alm, 1990; Guy et al., 2001). The transfer of paper birch populations outside of their seed source could therefore potentially affect their fitness. For instance, Wang et al. (1998) determined that birch provenances in a greenhouse experiment had different physiological responses to altering soil moisture and nutrient availability regimes. Even though all four populations were from British Columbia two of the provenances required high

water conditions in order to grow rapidly. In contrast, the water and nutrient strategies of the remaining two populations were more hardy allowing the plants to perform better under low water regimes indicating a higher degree of drought tolerance. Therefore, the environment in which these populations are transplanted could influence their growth rate or survival.

The Abitibi-Temiscamingue region is dominated by luvic gleysol (Government of Canada, 2013). Thus, these fertile soils are mainly composed of clay allowing for a slow diffusion of water over the course of the growing season (Government of Canada, 2013). Research suggests that abiotic factors strongly influence birch development (Possen et al., 2021), however, minimal studies have determined such effects on the structure and growth characteristics of paper birch in plantations in northwestern Quebec.

1.4 Approaches and techniques

1.4.1 Common garden experiments

Provenance trials are commonly used to comparatively analyze the degree of genetic variability and phenotypic plasticity that exists within species as a result of local adaptation to environmental conditions (Newton, 2007). Specifically, it allows for trait related responses pertaining to physiological strategies and morphology to be analyzed. Given that trees are grown under the same environmental conditions, differences between provenances would allude to genetic variability as a result of genetic assimilation at origin source. Contrarily, a lack of trait related difference would provide evidence of retained plastic ability within the genetic makeup of the provenances. This makes common garden experiments ideal for understanding how trees will respond to different environmental conditions after being relocated from their original locality.

Thus, we established five common garden experiments across Abitibi-Temiscamingue to capture variation between climate and edaphic characteristics (Figure 1.2).

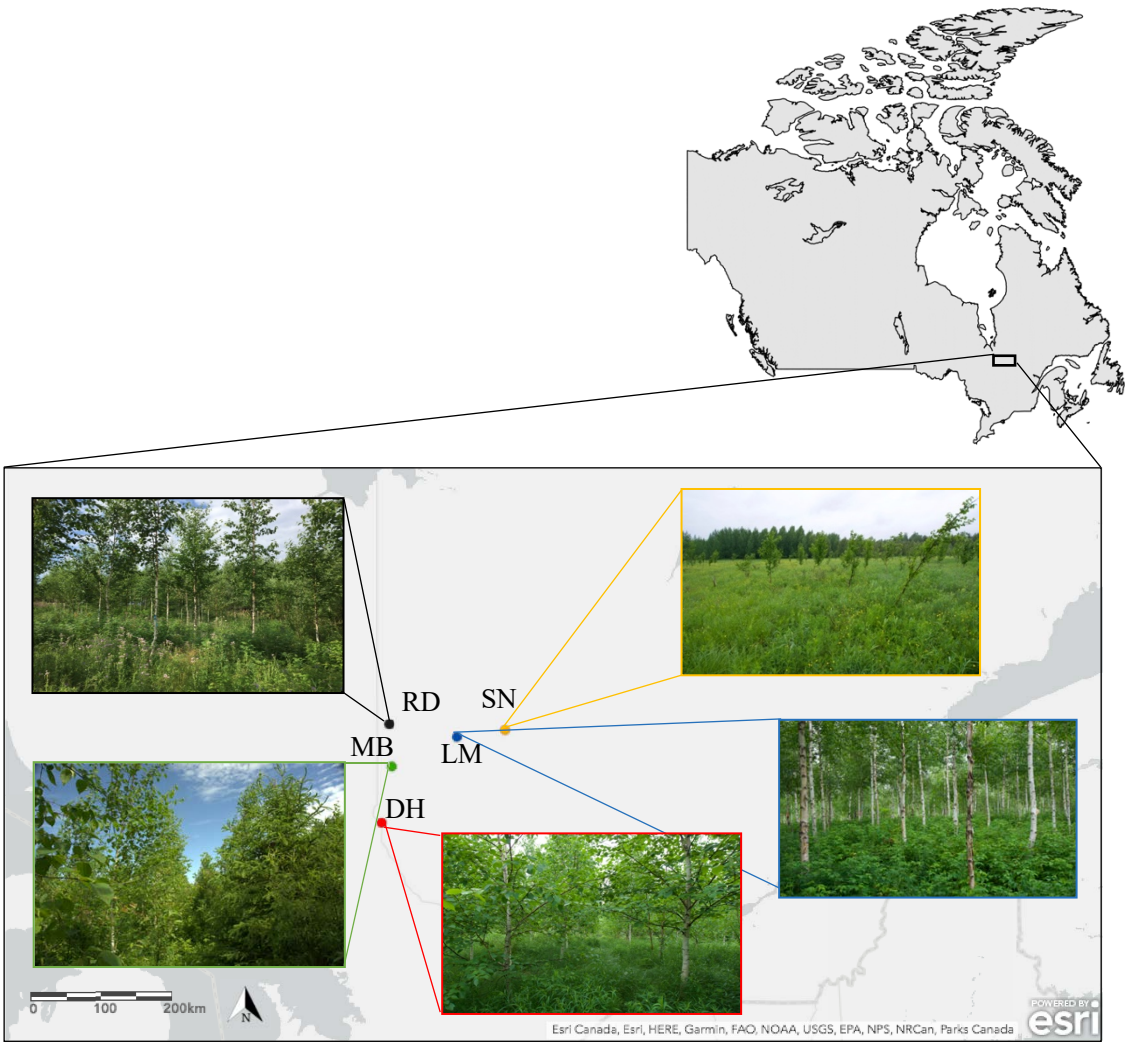

Figure 1.2 Common garden locations (RD – Rapide-Danseur, SN – Senneterre, LM – La Motte, DH – Duhamel-Ouest and MB - Montbeillard) across Abitibi-Temiscamingue.

1.4.2 Paper birch physiological strategies and environmental influence

To determine whether the physiological strategies of paper birch differed between provenances we analyzed gas exchange, foliar $\delta^{13}C$ and nutrient concentrations in addition to specific leaf area (SLA). Measuring leaf characteristics provides crucial to understanding plant resource requirements (Lambers et al., 2008; Peìrez-Harguindeguy et al., 2013), and their influence on tree growth. Photosynthesis is a process used by plants to fuel growth and development by synthesizing light energy into carbon compounds (Lambers et al., 2008). The energy stored in these complex compounds are used in various of cellular mechanisms and as a source of energy (Lambers et al., 2008). Thus, photosynthetic rate was used as a proxy for tree productivity. Comparatively, SLA is often used to capture a plant's resource acquisition strategy which is reflective of its environment (Wilson et al., 1999).

Measuring soil and foliar nutrient concentrations provides insight regarding the nutritional quality of the environment and paper birch's ability to extract nutrients from the soil. Macronutrients such as nitrogen (N; NH_4^+ and NO_3^-), phosphorous (P; $H_2PO_4^-$ and HPO_4^{-2}), potassium (K^+) are essential macronutrients for plant development (Day and Gurmani, 1993). A deficiency of these nutrients within the soil can lead to poor growth/development, increased susceptibility to infestation and when severely lacking mortality of birch (Hoyle and Bjorkbom, 1969). Nitrogen is a component of amino acids which are needed for building proteins. Thus, N deficiency can lead to a lack of cell division resulting in poor growth and development (Imran and Gurmani, 2011). Physiologically, foliar nitrogen content is often heavily correlated with SLA and photosynthetic activity (Peìrez-Harguindeguy et al., 2013). Thus, in addition to photosynthetic rate, leaf nitrogen content (N_{leaf}) was used to explain tree growth. P plays a crucial role in photosynthesis as it is a major component of plant energy ADP and ATP (adenosine di and triphosphate) (Schachtman et al., 1998). Further, P is a component of reproduction (i.e. flowers, in addition to seed and fruit development) and aids in root development (Schachtman et al., 1998). Influencing water use efficiency,

K regulates the opening and closing of stomata while translocating photosynthates for fruit and root storage or development (Humble and Hsiao, 1969; Singh et al., 2013). Capturing the foliar and soil nutrient concentrations at sites provides insight regarding provenance response to site quality.

During photosynthesis, the rate at which a plant loses water depends on physiological, morphological and environmental factors (Peìrez-Harguindeguy et al., 2013). To investigate paper birch's intrinsic water use efficiency (WUE), we used foliar carbon isotopes as an approximation of drought stress. Although, there is much debate surrounding the best method to estimate WUE, carbon isotopes reflect the relationship between CO_2 fixation and water loss (Dawson et al., 2002). Atmospheric concentrations of $^{13}C/^{12}C$ are higher than those found within plants, as a result plants actively discriminate against the heavier isotope ^{13}C resulting in depleted values of ^{13}C (Dawson et al., 2002). Therefore, increasing CO_2 assimilation results in decreased stomatal conductance and increased WUE (Picotte et al., 2007). Leaves lighter in mass contain more ^{12}C indicating CO_2 fixation occurs at a higher rate than water loss, whereas heavier leaves contain more ^{13}C, thus water is lost at a higher rate than CO_2 is fixed (O'Leary, 1988; Picotte et al., 2007). Understanding the isotopic ratio provides insight regarding water use strategy and their productivity between sites.

Edaphic variables strongly impact the morphological structure and physiological traits of paper birch (Hoyle and Bjorkbom, 1969), therefore, to estimate the degree of influence we measured the variability of nutrient and water availability between sites. Stunted growth and reduced stem quality can often be attributed to inadequate site characteristics (Singh et al., 2013). Thus, to effectively manage birch plantations it is essential to understand how environmental characteristics influence growth and productivity to ensure the highest potential yield. Tree height and diameter at breast height (DBH) were recorded to determine the quality of each provenance in regards commercial forestry based standards.

Soil characteristics such as texture and pH can impact root development and absorption of important macro and micronutrients. Compact clay soils impede root development by restricting the mobility and penetration of the primary root while altering the development of secondary roots (Gerard et al., 1972). In addition, high concentrations of clay can impede growth as phosphorous actively binds to minerals, thus impacting its availability (Guillemette and DesRochers, 2008; Ulen and Snall, 2007). Similarly, pH affects nutrient availability (Fernandez and Hoeft, 2009). Nutrients within acidic soils dissolve easily but contain less phosphorous, magnesium and calcium. Alkaline soils have nutrients that do not dissolve as easily and low absorption of manganese, phosphate, iron, zinc, boron and other micronutrients (Fernandez and Hoeft, 2009). Thus, a plants ability to obtain various nutrients can be impeded depending on soil pH.

1.4.3 Quantify the effect of translocating provenances to new environments

To measure the effect of translocating provenances along the clay belt from a source of origin we normalized climate data between 1970-2018 and created quadratic models. Data was provided by Natural Resources Canada's Canadian Forestry Service (CFS) and acquired using thin-plate smoothing splines within ANUSPLIN climate model software (McKenney et al., 2011). Climate variables such as precipitation, temperature and growing degree days were selected to test environmental influence as they are associated with plant growth and development. Within the quadratic models was a transfer function used to estimate the difference between provenance source environment and Abitibi-Temiscamingue. By using this function we were able to model whether transferring the provenances had a null, positive or negative effect on growth and survivorship. Thus, if provenances exhibited evidence of growth impediment or reduced survivorship, after translocation, it would insinuate the presence of inherent genetic traits. Conversely, if models predicted a positive or null influence, it could be theorized that provenances were able to adapt to the new conditions having retained plastic traits.

1.4.4 Investigating interspecific competition within plantations

Interspecific competition occurs when members of different species compete for resources in an environment (Goldberg and Barton, 1992). Plants often compete amongst others for light, water and soil nutrients (Aerts, 1999). To quantify the impact of competition from native species after translocating provenances, we conducted vegetation surveys. The degree and ability of paper birch provenances to compete with other species of flora will influence where plantations should be established. It also provides insight regarding how interspecific competitive influence alters tree productivity. If the presence of certain species impedes productivity such information will be useful for determining the degree of vegetative control needed to minimize competition in intensively managed plantations in Abitibi-Temiscamingue.

1.5 Research objectives & significance

The purpose of this study was to assess and compare the growth and physiology of paper birch provenances planted at multiple sites in a common garden experiment across the region of Abitibi-Témiscamingue. To investigate whether paper birch from various regions of Quebec exhibited phenotypic plasticity or genetic assimilation, we measured physiological strategies and environmental variables impacting the growth and establishment of paper birch in a common garden experiment. Further, we aimed to understand how translocating populations from different ecological regions impacted the productivity of provenances. The specific objectives of the study were to 1) identify the natural variability of phenotypic and physiological characteristics and 2) characterize the eco-physiological and environmental factors influencing rapid establishment, growth and morphology of paper birch provenances in plantations under intensive management.

Seed sources were collected from three different vegetation zones (continuous boreal forest subzone, mixed forest subzone and hardwood forest subzone). Morphological differences were expected to be strongest between the northernmost and southernmost seed sources as we hypothesized provenances would have acclimated to their seed origin environments (north – colder and shorter growing seasons vs. south – warmer and longer seasons). We predicted leaf characteristics such as SLA would reflect the environmental conditions of provenance seed origin. Further, leaf morphology was expected to influence water use efficiency and photosynthetic capability. Research indicates that species with high specific leaf area have high stomatal conductance, which allow the plant to achieve high rates of photosynthesis (Chapin and Eviner, 2003). However, as a result these plants do not use water efficiently making them susceptible to drought. Thus, we hypothesized that provenances from areas with high water retention capabilities would have high SLA and photosynthetic rates.

The results gathered from this study will benefit the Canadian forestry sector and increase the profit margins of private woodlot owners who have been targeted for the establishment of fast-growing, high-quality wood plantations in Quebec. Further, the province has been utilizing breeding programs to genetically improve species (Rainville, 2003). Thus, the high degree of phenotypic variation within paper birch populations is preferable when selecting for the most advantageous traits. The improvement of paper birch could potentially create a complex that is more efficient in terms of quality and growth, which aligns with current sustainable management practices while increasing economic gain.

CHAPTER II

ASSESSING THE PLASTICITY OF PAPER BIRCH TRAITS IN A BOREAL COMMON GARDEN EXPERIMENT

Jenna M. Rabley, Philippe Duval and Annie DesRochers

To be submitted to the journal of Forest Ecology and Management.

2.1 Abstract

Studies have identified plasticity variation within paper birch (*Betula papyrifera*) functional traits due to its wide natural distribution and large degree of genetic diversity, allowing for competitive local adaptation and varying physiological characteristics. In order to investigate the eco-physiological and environmental factors influencing rapid establishment, growth and the morphology of paper birch, we designed a common garden experiment with five sites at differing latitudinal locations across northwestern Quebec, Canada. Net photosynthesis, foliar nutrient concentration (N, K and P), specific leaf area (SLA), leaf carbon isotope composition ($\delta^{13}C$), growth characteristics and edaphic variables were measured for each provenance at each site. Climate data was normalized over a 30+ year trend, from 1970-2018, and used to determine the effect of translocating provenances. After 10 years of growth, we found significant differences among provenance mean tree DBH and survivorship across sites. Provenance resource acquisition strategies exhibited strong evidence of phenotypic plasticity as productivity was largely influenced by site quality. Productive sites were characterized by phosphorous availability and slightly acidic soils. Additionally, growth was negatively influenced by heavy clay and interspecific competition. Translocating provenances from various vegetation zones across Quebec had a null effect on productivity, further exemplifying the role of phenotypic plasticity in paper birch adaption mechanisms. The findings gathered from this study will benefit the Canadian forestry sector and increase the profit margins of private woodlot owners who have been targeted for the establishment of fast-growing, high-quality wood plantations.

Keywords : paper birch, provenance transfer functions, common gardens, carbon isotopes, foliar nutrients, phenotypic plasticity

Résumé

Des études ont identifié une variation de plasticité dans les traits fonctionnels du bouleau à papier (*Betula papyrifera*) en raison de sa large distribution naturelle et de son grand degré de diversité génétique, permettant une adaptation locale compétitive et des caractéristiques physiologiques variables. Afin d'étudier les facteurs éco-physiologiques et environnementaux influençant l'établissement rapide, la croissance et la morphologie du bouleau à papier, nous avons conçu une expérience en jardin commun avec 8 provenances sur cinq sites distribués en latitude à travers l'Abitibi-Témiscamingue. La photosynthèse nette, la concentration en nutriments foliaires (N, K et P), la surface foliaire spécifique (SFS), la composition isotopique en carbone foliaire ($\delta^{13}C$), la croissance et les variables édaphiques ont été mesurées pour chaque provenance à chaque site. Les données climatiques ont été normalisées sur une tendance de 30+ ans, de 1970 à 2018, et utilisées pour déterminer l'effet de la translocation des provenances. Dix ans après la plantation, la taille moyenne et le taux de survie des provenances différaient entre les sites. Les stratégies d'acquisition de ressources des provenances ont montré de solides preuves de plasticité phénotypique, la productivité étant largement influencée par la qualité du site. Les sites productifs étaient caractérisés par une plus grande disponibilité en phosphore et des sols légèrement acides. De plus, la croissance a été négativement influencée par l'argile lourde et la compétition interspécifique. La translocation de provenances de diverses zones de végétation à travers le Québec a eu un effet nul sur la productivité, illustrant davantage le rôle de la plasticité phénotypique dans les mécanismes d'adaptation du bouleau à papier. Les résultats de cette étude profiteront au secteur forestier canadien et augmenteront les marges bénéficiaires des propriétaires de boisés privés qui ont été ciblés pour l'établissement de plantations d’essences à croissance rapide et de haute qualité au Québec.

Mots clés : bouleau blanc, fonctions de transfert de provenance, jardin commun, isotopes de carbone, nutriments foliaires, plasticité phénotypique

2.2 Introduction

Although an ecological and economically profitable species, paper birch (*Betula papyrifera* Marsh.) remains understudied in Canada. The species is characterized as a shade intolerant, deciduous broad leaf tree, with a vast natural distribution across North America (Perala and Alm, 1990). Known as a pioneer species, paper birch grows over a wide range of climatic and edaphic conditions (Safford et al., 1990). The vigorous growth rate and successful establishment of this hardwood species provides interesting economic opportunity within the commercial forestry sector. Recently, paper birch has been utilized by industries to make wood products such as veneer, flooring and furniture (Rainville, 2003). However, this resource can also be used for the production of pulp, lumber and specialty products (Rainville, 2003). The value of this species may yet increase as studies have identified paper birch as a potentially beneficial addition to mixed-conifer stands when planted in small volumes (Jõgiste, 1998; Simard and Vyse, 2006). Birch leaves are rich in important macro and micronutrients, thus increasing the soil nutrient availability when they decompose (Welke and Hope, 2005; Safford et al., 1990; Saetre, 1999).

Spanning across various Canadian ecozones (Safford et al., 1990), populations of paper birch have been exposed to different selection pressures resulting in a plastic gene pool (Safford et al., 1990). In addition, natural hybridization between individuals is common, thus increasing the degree of genetic diversity (Hawkins and Dhar, 2012; Pyakurel and Wang, 2014). Such diversity is useful to silvicultural practice as it enhances the ability to manipulate genes in order to maximize growth and quality of wood in intensively managed plantations (Hart, 2010). Plasticity within the gene pool arising from different environmental pressures can influence the survival and development of trees (Pigliucci et al., 2006; Sultan, 2000). Therefore, understanding

the influence of local adaption can aid in the forestry industry's ability to plan where plantations should be grown and managed.

The phenotypic plasticity and genetic structure of a trait influence observable differences in physiological performance (Nicotra and Davidson, 2010) and the phenotypic expression between plant populations of the same species across various environments (Pigliucci, 2006). Species distributed along an environment gradient can exhibit a genotype able to express multiple phenotypes (i.e. phenotypic plasticity), however, such responses are specific to a particular trait function like nutrient uptake (Sultan, 2000). Alternatively, traits that have been exposed to consistent environmental conditions over a series of generations can undergo genetic assimilation and become locally adapted to a particular area (Pigliucci, 2006; Lascoux et al., 2016). The response of such traits becomes a reflection of their local environment, making these individuals more susceptible to negative impacts in the presence of rapid changes within the ecosystem as a result of environmental stress (Aitken et al., 2008; Gao et al., 2018). Differences in phenology (Hawkins and Dhar, 2012; Pyakurel and Wang, 2014) and physiological strategies (Benowicz et al, 2001; Wang et al., 1998) of paper birch have been observed in various studies indicting high genetic variability depending on provenance origin. Thus, further investigation is required to understand how transferring the species will impact their performance across Canada.

We established five common garden experiments across northwestern Quebec to investigate the variability of adaptive traits from eight paper birch populations. The natural populations were spread across a latitudinal gradient within Quebec. The purpose of the study was to (1) identify the natural variability of morphological and physiological characteristics and (2) characterize the eco-physiological and environmental factors influencing rapid establishment, growth and leaf morphology of paper birch provenances in plantations under intensive management.

Due to the wide dispersal of paper birch across various vegetation zones we expected the results of this study to exhibit evidence of local adaption between populations. In

theory, functional traits driving the productivity of populations should display some form of resource acquisition trade-off given the differing environmental conditions between regions (Reich, 2014). Thus, we expected provenances to have acclimated to their seed origin environments with the greatest degree of difference occurring between resource rich populations in southern latitudes (warmer and longer growing season) and populations in northern latitudes (colder and shorter growing season). Southern regions of Quebec receive higher rates of precipitation than the north. Research by Pyakurel and Wang (2014), indicated that paper birch accustomed to areas with elevated rates of precipitation are reflected by higher photosynthetic capacities. However, the trade-off of this strategy may result in an increased sensitivity to drought (Chapin and Eviner, 2003; Reich, 2014). Therefore, we expected southern provenances to outperform their northern counterparts by demonstrating greater photosynthetic rate and exhibit increased rates drought tolerance due to the moisture capacity of clay soil in northwestern Quebec. In addition, we expected to see provenance variation reflected by different physiological strategies and growth rates within plantations, as a result of local adaptation to their seed origin. The results gathered from this study will benefit the Canadian forestry sector and increase the profit margins of private woodlot owners who have been targeted for the establishment of fast-growing, high-quality wood plantations in Canada.

2.3 Methodology

2.3.1 Study area and seed origin

Seeds were collected from eight natural populations of paper birch spread across various regions of Quebec including Abitibi-Témiscamingue, Mauricie, Laurentians and Outaouais (Figure 2.1). Seeds were acquired from three separate parent trees for each of the eight provenances, which were chosen to represent the genetic variation across the interior region of Quebec.

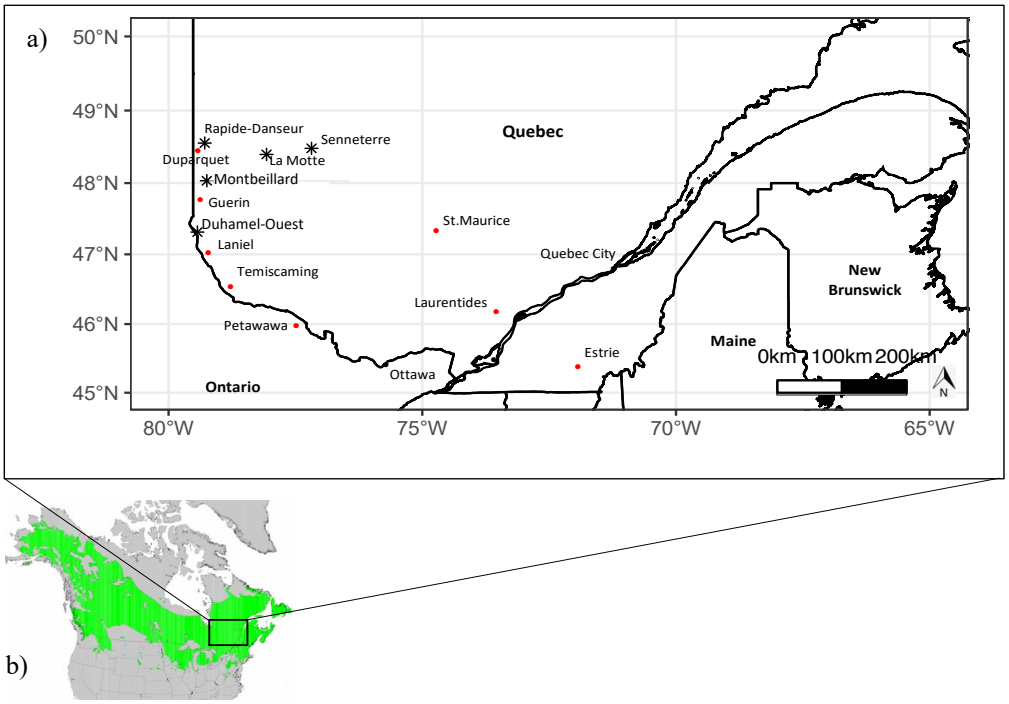

Figure 2.1 (a) Distribution of sites, denoted as stars, across Abitibi-Temiscamingue and provenances, shown in red, across Quebec. Ottawa and Quebec City are provided for perspective. (b) Map from the United States Department of Agriculture, Natural Resources Conservation Service (https://plants.usda.gov/core/profile?symbol=BEPA) outlining the distribution of paper birch across North America.

In the spring of 2008, one year old seedlings previously grown at a greenhouse in Berthierville (46° 05' 00.51" N, 73° 11' 05.13" W), were planted at five abandoned agricultural fields across northwestern Quebec including La Motte (LM), Montbeillard (MB), Rapide-Danseur (RD), Senneterre (SN) and Duhamel-Ouest (DH) (Figure 2.1). Seedlings were grown in 340cc containers and ranged from 46-56cm at the time of planting. Each plantation was ploughed in the fall and harrowed in the spring before planting, with the exception of Montbeillard due to time restrictions. This site was both ploughed and harrowed in the spring before planting. In addition, all sites excluding La Motte were treated with glyphosate in the summer before ploughing at the request of the stakeholder.

Each experimental plantation was composed of four replicate blocks with eight provenances in each block and 9 to 16 individuals per provenance. Spacing was 2.5 m × 2.5 m between trees. Plantation sites of La Motte and Senneterre were greater in size and contained 128 trees per block and 512 individuals per site (1 site = 4 replicate blocks × 8 provenances × 16 individuals). Additional paper birch were planted surrounding the blocks to create a buffer zone in attempts to reduce edge effect at all sites.

Spread across a considerable latitudinal gradient, study plantations are distributed across various climate zones within Abitibi-Temiscamingue. However, climate was relatively similar between sites (Table 2.1) with each characterized by mean temperatures during the coldest months around -22.6 to -25.1˚C and warmest months at 23.5 to 24.9˚C. Given the relatively cold winters and warm summers of the region, the mean annual temperature is just above 0, ranging from 1.5 to 3.4˚C. Mean precipitation during the growing season varies narrowly across sites. Montbeillard and Rapide-Danseur receive slightly lower rates of rainfall (474 and 481mm) in comparison to Duhamel-Ouest, La Motte and Senneterre (511, 516 and 567mm). Being the most southern location, Duhamel-Ouest's growing season is two weeks longer than the other plantation site.

Spread across a maximum of 3º of latitude and 8º of longitude, provenances belong to distinct ecological regions in Quebec. The most northern provenance Duparquet, is characterized by a shorter growing season with roughly 1323 days above 5°C, cold winters with an average temperature of 24.6°C during the coldest months and warm summers with an average of 23.8°C during the summer months. In contrast, southern provenances like Estrie and Petawawa have longer growing seasons with 1677 and 1770 growing degree days above 5°C, mild winters with averages of -16.9°C and -19.3°C and warm summers with averages of 24.6°C and 26.3°C (McKenney et al., 2011).

Table 2.1 Geographic locations listed from north to south and climate characteristics of the eight provenances planted at the five sites across northewstern Quebec, Canada.

Location	Latitude	Longitude	E	MAT	DD >5°C	MTCP	MTWP	MSP	ATR	DGS
Provenances										
Duparquet	48° 28' 1" N	-79° 24' 7" W	309	1.7	1323	-24.6	23.8	488	48.2	170
Guerin	47° 46' 38" N	-79° 21' 18" W	308	2.4	1402	-24.3	24.4	474	43.3	174
St-Maurice	47° 20' 30" N	-74° 42' 15" W	472	2.3	1317	-22.8	23.3	626	45.6	173
Laniel	47° 1' 46" N	-79° 11' 45" W	271	3.6	1537	-21.6	24.7	532	46	185
Temiscaming	46° 33' 7" N	-78° 45' 21" W	293	4.1	1593	-20.2	25.1	538	44.9	189
Laurentides	46° 11' 40" N	-73° 31' 15" W	184	4.8	1722	-19.3	25.7	617	44.5	191
Petawawa	45° 51' 36" N	-77° 23' 24" W	182	5.1	1770	-19.3	26.3	516	45.1	195
Estrie	45° 23' 15" N	- 71° 54' 30" W	315	5.3	1677	-16.9	24.6	696	41	198
Plantation Sites										
Rapide-Danseur	48° 33' 18" N	79° 18' 54" W	280	1.5	1282	-24.7	23.9	480	48.6	169
Senneterre	48° 28' 51.6" N	74° 10' 58.8" W	313	1.6	1277	-25.1	23.5	567	48.2	169
La Motte	48° 23' 52.8" N	75° 4' 12" W	314	1.6	1277	-25	23.7	516	48.4	169
Montbeillard	48° 1' 58.8" N	79° 14' 52.8" W	273	2.3	1399	-24.7	24.4	474	48.8	173
Duhamel-Ouest	47° 18' 50.4" N	79° 25' 55.2" W	228	3.4	1548	-22.6	24.9	511	47.1	183

Note: Abbreviations are as follows: E – elevation; MAT – mean annual temperature (ºC); DD>5 ºC – degree days >5 ºC; MTCP – mean temperature of the coldest period (ºC); MTWP – mean temperature of the warmest period (ºC); MSP – mean precipitation in summer (mm); ATR – annual temperature range (difference between the maximum temperature of the warmest period and minimum temperature of the coldest period) (ºC); DGS – number of days in the growing season.

2.3.2 Field measurements

Ecophysiological characteristics

Tree height and diameter at breast height (DBH) were measured for each individual in addition to survivorship at each site in the summer of 2018. Leaf net photosynthetic rate (P_N) was measured at the beginning of August in 2019, from 07h00 until disruption in photosynthetic activity was observed due to heat stress. Three trees were randomly selected per provenance for each block at each site (n = 480, 3 trees × 8 provenances × 4 blocks × 5 sites). One fully developed and illuminated outer leaf from the upper canopy facing south was selected and measured using a CIRAS-2 portable photosynthetic system and broadleaf cuvette (PP-Systems, MA, USA). The cuvette was equipped with a LED light attachment to ensure leaves were exposed to 1000 µmol m^2s^{-1} of photosynthetically active radiation (PAR). The reference CO_2 was set to 350 µmol m^{-1} with a flow rate of 200 µmol s^{-1} in the broadleaf cuvette chamber. Following the measurement, three healthy leaves from the same branch were retained and stored in a cooler until leaf area could be measured using a Li-Cor 3100 area meter (Lincoln, NE, USA). Therefore, nine leaves were kept per provenance per block. After the leaves were dried at 80°C for 48 hours their dry mass was recorded and specific leaf area (SLA) was calculated as leaf area divided by dry weight.

Leaves from the same provenance and block were ground together to a fine powder using a ball mill (Retsch MM301, DE-NW, Germany) for two minutes. Foliar nitrogen (N) and total carbon isotope ($\delta^{13}C$) concentrations were determined using a PDZ Europa ANCA-GSL elemental analyzer interfaced to an isotope ratio mass spectrometer at the University of California Davis Stable Isotope Facility (UCD SIF; Davis, CA, USA). Carbon isotope concentrations were calculated as:

$$\delta^{13}C = [(R_{sample}/R_{standard})\text{-}1000]\times 1000 \quad (2.1)$$

where R_{sample} and $R_{standard}$ are the ratios of $^{13}C/^{12}C$ in the sample and standard. Composition was calculated using Vienna PeeDee Belemnite as a standard. A portion of the ground leaf samples were retained and sent to the Analytical Chemistry Services Laboratory (NRL; Victoria, BC, CA). Foliar concentrations of potassium (K), phosphorous (P), sulfur (S), calcium (Ca), magnesium (Mg) and zinc (Zn) were analyzed using inductive coupled plasma mass spectrometry (ICP-MS). Samples were prepared in a closed vessel microwave and digested in nitric acid (HNO_3)/ hydrochloric acid (HCl).

2.3.3 Site quality

In 2018, a Dutch Auger was used to extract soil cores at a 20 cm depth from the centre of each provenance in each block. The soil was oven dried at 70°C or 72 hours. Slope was measured in the centre of each provenance within each block. In 2019, soil texture was determined using the United States Department of Agriculture – Natural Resources Conservation Service flow diagram to measure texture by feel (USDA-NRCS 1999).

To characterize the availability of inorganic soil nutrients such as N, P, K, iron (Fe) and Ca, soil samples were analyzed at the Analytical Chemistry Services Laboratory (NRL; Victoria, BC, CA). Total nitrogen was evaluated using an elemental analyzer (Flash 2000, Thermo Scientific, NRL). All other nutrients were extracted via Mehlich III extraction and analyzed using inductively coupled plasma-optical emission spectroscopy (ICP-OES, NRL).

Soil pH was examined using an Accumet AR50 pH meter (Fisher Scientific, NH, USA). We measured two grams of soil into a beaker and mixed it with 20 grams of distilled water. The soil was stirred occasionally over the course of 30 minutes.

To measure the effect of interspecific competition within plantations, a vegetation survey was conducted for each provenance in each block (n = 32 per site). Provenances

were sectioned into four quadrants, each containing 25% of the total surface area. Species were identified and categorized as angiosperm/vascular, graminoid, bryophyte or a woody (i.e. tree or shrub) plant. Percent ground cover was cumulated between quadrants to account for 100% of the area within each provenance.

2.3.4 Climate variables

Our analysis was composed of seven climate variables and two geographic variables; mean annual temperature (MAT), maximum temperature during the warmest month (MTWP), minimum temperature during the coldest month (MTCP), the annual temperature range (difference between the maximum temperature of the warmest period and minimum temperature of the coldest period; ATR), number of growing degree days above 5ºC (DD >5°C), mean summer precipitation (MSP), mean annual precipitation (MAP), elevation and latitude.

Climate variables were chosen to describe the general climate of the seed origin and plantation locations. Thus, we chose variables that are known to heavily influence plant growth and development. Weather records were provided by Natural Resources Canada's Canadian Forestry Service (CFS), normalized between 1970-2018 (McKenney et al., 2011).

2.3.5 Data analysis

A mixed effect ANOVA was used to determine whether rates of survivorship, stand volume and mean tree DBH changed across site. Models were also used to examine whether provenances differed in regards to their physiological strategies. To account for the complex structure of our data and hierarchical nature of the experimental design site, block and provenance were specified as random terms with provenance nested within block and block nested within site. However, due to the lack of replicates in the

models explaining the effects on foliar nutrients and isotopic composition only site and block were used as random terms (n = 4 samples per provenance per site). To determine whether the effects of provenance were directly related to the influence of site we used an interaction term. A Tukey's HSD post-hoc analysis was performed on models that rejected the null hypothesis to note significant differences between groups.

Exploratory linear mixed effect models were designed to evaluate the effect of abiotic influence on the mean DBH, survivorship and stand volume of paper birch. Block nested within site was included as a random term to account for (1) the hierarchy of the experimental design and (2) complexity of the data. Stand volume was calculated as follows:

$$Sv_{(j(l(i)))} = Tv \times (s \times 1600) \tag{2.2}$$

Sv is the stand volume in the *j*th block at the *l*th site for the *i*th population. The survivorship (s) is calculated as the number of living trees divided by the number that were planted. This is multiplied by area per hectare. Tree volume is presented as Tv and is calculated as follows:

$$Tv_{(j(l(i)))} = 0.33 \times \left(\left(\frac{DBH}{2}\right)^2 \times \pi\right) \times h \tag{2.3}$$

where tree volume (Tv) is calculated per provenance (*i*) based on block (*j*) and site (*l*). *DBH* stands for diameter at breast height (m), while *h* denotes the height (m). The form factor is presented as 0.33 to account for the tapering of tree stems and conic shape (Husch et al., 2002).

To investigate and visualize the dynamics between (1) physiological strategies and (2) abiotic factors we used principal component analysis (PCA). Components that explained up to 80% of the variation within the data were retained. To explain

additional variation within the data, we grouped points, representing provenances, by site and overlaid groups with confidence ellipses of 95% on the PCAs.

To characterize the effect of translocating provenances we designed models with a quadratic function. We incorporated block nested within site as random terms to account for the complexity of the experimental design within the data and to exclude variation that is not explained by our fixed effects. The model is shown below as:

$$Y_i = b_0 + b_1X_1 + b_2X_1^2 + (r_s : r_b) + e \quad (2.4)$$

Where Y_i represents the DBH or survivorship, b_0 is the intercept, $b_{1\text{-}2}$ are the regression coefficients, X_1 is the effect of translocating provenances (site climate minus seed origin environment), r_s is the random effect site, r_b is the random effect block and e is the residual.

Growth variables not following a parametric distribution were normalized using log or square root transformations. Further, all predictor variables used in linear mixed effect and quadratic models were standardized to eliminate scaling issues. All statistical analyses were performed using R v.3.6.3 (R Development Core Team, 2020) with a focus on understanding outcomes at the provenance level.

2.4 Results

2.4.1 Growth and establishment

Variability among provenance survivorship within and across sites was dependent on site due to an interaction (P <0.001; Table 2.2; Figure 2.2). Sites with high productivity, DH and LM, exhibited low rates of mortality and less variability between groups.

Conversely, provenance survivorship was highly variable at all other sites. Southern provenances such as Estrie, Petawawa and Laurentides suffered from high mortality rates at the sites MB and RD, while Duparquet and St. Maurice shared some of the highest rates of survivorship. Similarly, the provenance Estrie had lower survivorship at the site SN (mean of 74%) in comparison to the northern provenances Duparquet (mean of 86%) and St. Maurice (91%) (Table 2.3).

After 10 years of growth, mean DBH (cm) and stand volume (m^3ha^{-1}) of paper birch varied significantly across sites ($P < 0.001$) but not among provenances ($P > 0.05$). Of the five plantation sites, LM had the highest stand volume (15.33 m^3ha^{-1}) and tallest birch trees with an average DBH of 7.3 cm and 6.8 m in height (Table 2.3). In contrast, SN had the smallest trees with an average DBH of 2.2 cm and lowest stand volume (0.66 m^3ha^{-1}). Trees at MB, RD and SN shared low rates of survival and growth while the plantation at DH, although significantly different from the previous three groups, had marginally higher stand volume (Table 2.3). Although RD, SN and MB had some large diameter trees, stand volume remained low as a result of poor survivorship (Figure 2.3). Particularly for SN where half the site was characterized by small trees in addition to low survivorship. In contrast, LM significantly differed from all other sites with large diameter trees and high survivorship, reflected by high stand volume.

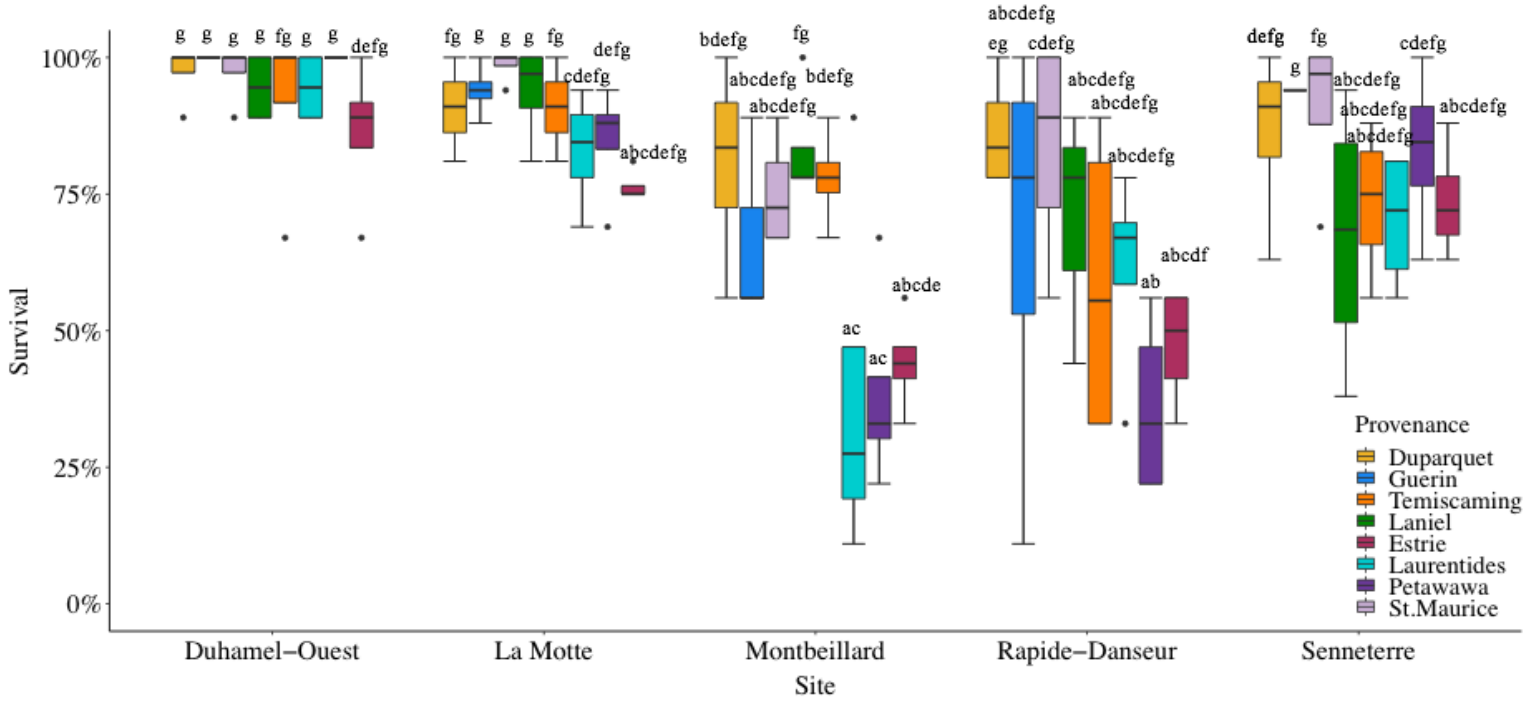

Figure 2.2 Boxplot outlining the interaction between provenance and site survivorship and their significant differences ($P < 0.05$) noted by differing letters. Standard error is present for each provenance in addition to the outliers and black lines denoting the median.

Table 2.2 Summary of ANOVA outputs listed with the degrees of freedom (d.f.) for each growth characteristic including mean diameter at breast height (DBH), stand volume (SV) and survivorship (S), in addition to the physiological strategies; specific leaf area (SLA), total photosynthetic rate (P_N), carbon isotopic ratio ($\delta^{13}C$), foliar nitrogen (Foliar N), phosphorous (Foliar P), potassium (Foliar K), magnesium (Foliar Mg), zinc (Foliar Zn) and calcium (Foliar Ca) concentrations.

		Growth			**Physiological Strategy**								
Source of Variation	d.f.	DBH	SV	S	SLA	P_N	$\delta^{13}C$	Foliar N	Foliar P	Foliar K	Foliar Mg	Foliar Zn	Foliar Ca
Provenance	7	0.17	0.71	<0.001	<0.001	0.04	<0.001	0.25	0.78	0.01	<0.001	0.01	1
Site	4	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.005	<0.001	1
Provenance x Site	28	0.83	0.85	0.001	0.19	0.31	0.005	0.47	0.94	0.14	0.01	0.003	1

Note: Significant difference at $P \leq 0.05$.

Table 2.3 Summary detailing the mean tree diameter at breast height (DBH) in cm, stand volume (SV) in m^3ha^{-1} and percent survivorship (S) for each provenance at each site.

Note: Significant difference at $P \leq 0.05$.

Provenance	Duhamel- Ouest			La Motte			Montbeillard			Rapide-Danseur			Senneterre		
	DBH	SV	S	DBH	SV	S	DBH	SV	S	DBH	SV	S	DBH	SV	S
Duparquet	4.37	4.28	97	6.76	13.36	91	3.36	1.87	83	3.35	2.09	89	1.99	0.63	86
Estrie	5.51	7.08	89	7.52	14.78	77	2.79	0.59	46	3.23	1.07	49	2.16	0.53	74
Guerin	4.89	5.93	100	7.49	16.86	94	4.37	3.25	54	4.03	2.10	80	2.14	0.70	94
Laniel	4.94	5.32	94	7.45	16.28	94	3.45	1.97	86	3.72	2.24	57	2.39	0.71	67
Laurentides	4.72	4.86	94	7.59	15.02	83	3.61	1.24	37	3.72	1.98	63	2.25	0.64	70
Petawawa	5.36	7.16	100	8.29	18.43	84	3.29	0.77	40	3.85	1.14	37	2.36	0.77	83
St-Maurice	4.78	4.93	97	6.65	13.29	98	3.80	2.52	77	3.95	3.11	86	2.22	0.75	91
Temiscaming	4.71	5.38	92	7.16	14.62	91	3.70	2.41	80	3.55	1.72	60	2.16	0.56	74

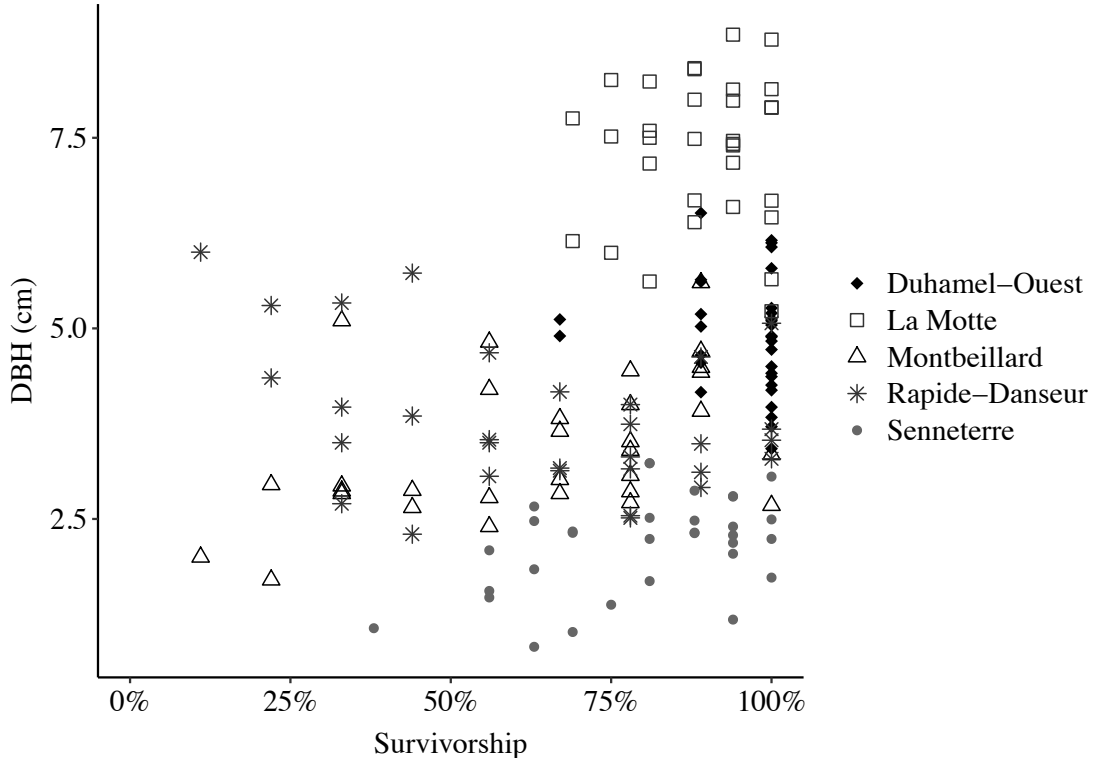

Figure 2.3 Relationship between mean diameter at breast height (DBH) and survivorship at each site location. Measurements were recorded after 10 years of growth.

2.4.2 Leaf functional traits

Specific leaf area (SLA)

Leaf morphology varied significantly among provenances (P <0.001) and across sites (P < 0.001), without an interaction between the two factors (Table 2.2). Post-hoc analysis revealed contrasts between mid and southern provenances with southern locations displaying slightly higher SLA than provenances from mid-latitudes (Figure 2.4; Figure A 1.a). Trees at La Motte had the highest SLA values while trees at Duhamel-Ouest had the lowest SLA values (Figure A 1.b).

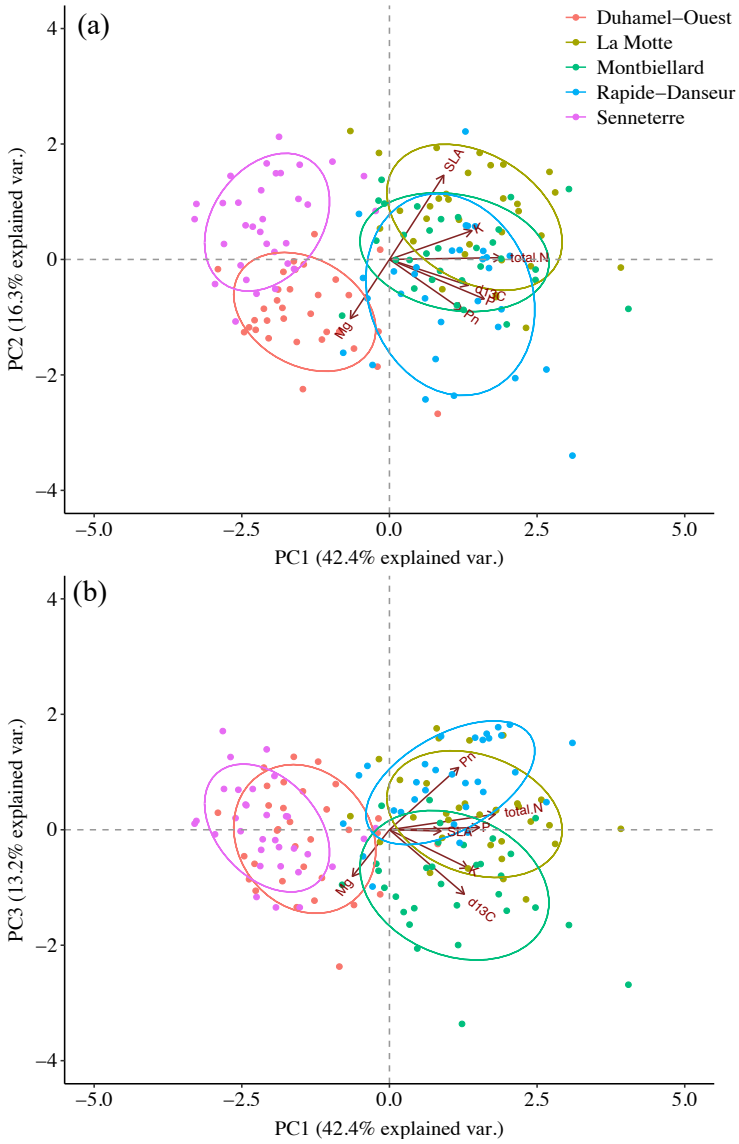

Figure 2.4 Principal component analysis sectioning traits of paper birch into gradients that explain physiological strategies between sites. (a) PC1 plotted against PC2 from a PCA, where PC1 is driven by foliar nitrogen (total.N), phosphorous (P) and potassium (K). PC2 is driven by SLA and foliar concentrations of Mg. (b) PC1 plotted against PC3, where PC3 is driven by total photosynthetic rate (P_N) and $\delta^{13}C$ (d13C).

Leaf net photosynthetic rate (P_N)

Although results from the mixed effect ANOVA indicated a significant difference between provenances in their punctual P_N (P= 0.04), post-hoc analysis did not reveal such differences. Thus, the marginal significance produced by the ANOVA is likely to be that of a type 1 error. There were however significant differences in P_N between sites (P <0.001), with the greatest difference between the two most northern sites Senneterre (mean of 9.70 µmol $m^{-2}s^{-1}$) and Rapide-Danseur (mean of 15.96 µmol $m^{-2}s^{-1}$; Figure 2.4). Photosynthetic rate was not significantly correlated to SLA (Figure A 2.a; r = 0.03, P = 0.6) or $\delta^{13}C$ (r = 0.13, P = 0.09), however, there was a moderate correlation to mean tree DBH (Figure A 2.b; r = 0.24, P = 0.002).

Carbon isotope ratios ($\delta^{13}C$)

There was a significant interaction between site and provenance for $\delta^{13}C$, indicating a trend could not be established for provenance discrimination of ^{13}C across sites (Table 2.2). Provenance water use efficiency was similar between Senneterre (-26.92 to -29.01‰), Rapide-Danseur (-26.42 to -28.69‰) and Duhamel-Ouest (-26.2 to -28.67‰), while trees at La Motte (-25.63 to -28.36‰) and Montbeillard (-24.76 to -27.98‰) were slightly less efficient. However, this is not to say that all provenances behaved the same between sites. Southern provenances, Estrie and Petawawa, appeared to have lower water use efficiency at Montbeillard compared to other sites (Figure 2.5). In contrast, Duparquet, the northern provenance maintained similar fixation rates across sites. Mean tree DBH was not correlated with $\delta^{13}C$ (r = 0.12, P = 0.12), mainly because trees at Rapide-Danseur had high P_N rates but low tree DBH.

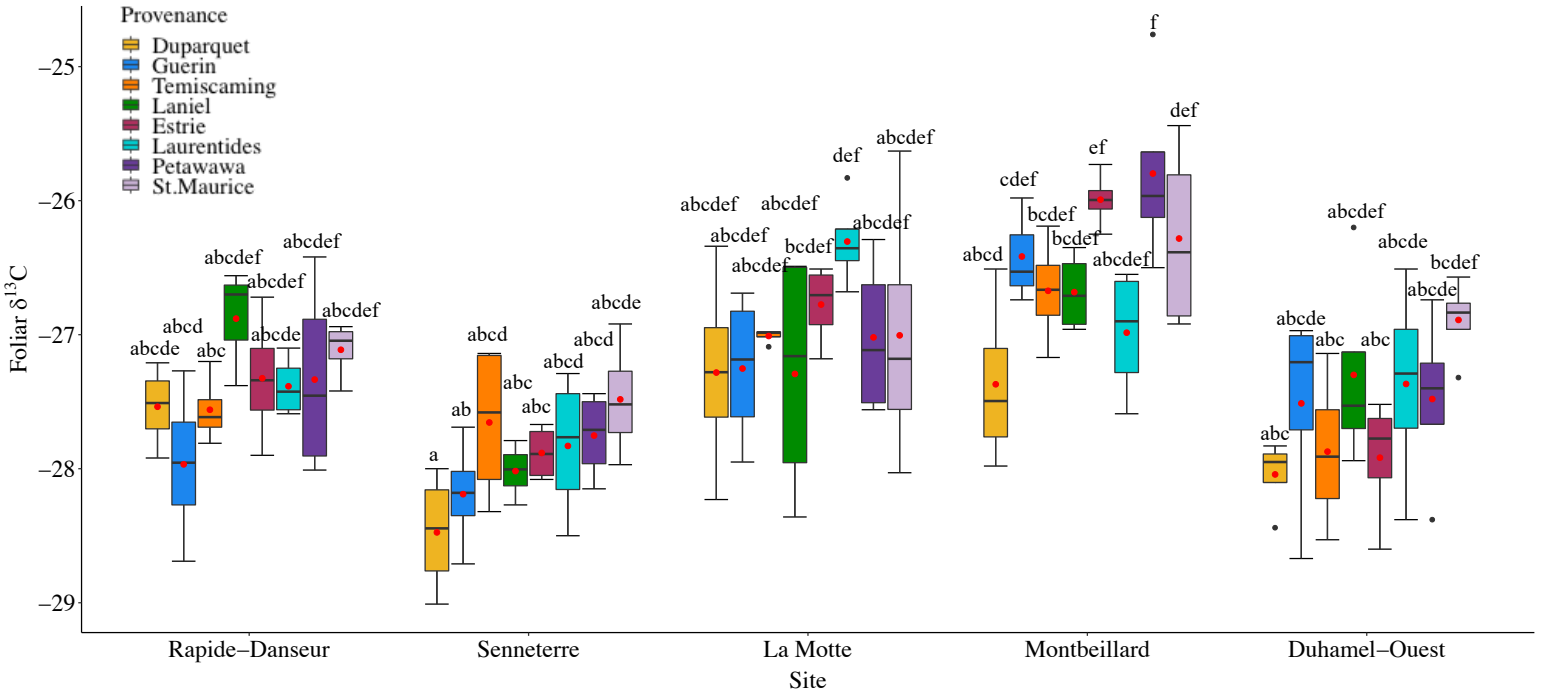

Figure 2.5 Boxplots outlining the variance in foliar carbon isotope ratios (δ13C) and the significant differences between provenances and sites. Significant differences among provenances at $P < 0.05$ are noted by different letters. Black lines within each box represent the median while the red dots denote the mean value. The standard error is present for each provenance across sites in addition to the outliers.

Foliar nutrients

Foliar nutrient concentrations varied depending on location ($P < 0.001$, Table 2.2). Potassium (K), magnesium (Mg) and zinc (Zn) differed between provenances, however, such differences could not be identified for zinc, likely due to a type 1 error. N_{leaf} was positively correlated to P_N (r = 0.58, $P < 0.001$), DBH (r = 0.52, $P < 0.001$), P (r = 0.65, $P < 0.001$) and $\delta^{13}C$ (r = 0.52, $P < 0.001$). The highest N_{leaf} concentrations were found at La Motte (9.58% to 14.43%). Inversely, Senneterre and Duhamel-Ouest were characterized by lower levels of N (SN 6.83% to 9.65%, DH 7.61% to 10.41%) and contained significantly lower concentrations of P, K and Zn ($P < 0.001$) in comparison to the other sites. Although lacking other foliar nutrients, these sites were characterized by higher Mg uptake. Trees at Rapide-Danseur and Montbeillard had similar N_{leaf} concentrations ranging 8.39%-12.45%, in addition to having the greatest uptake of foliar Zn. Following a similar pattern, P and K were abundant in leaves at La Motte and Rapide-Danseur.

Functional traits

Functional traits were explained along three axes in a principal component analysis (PCA), cumulatively explaining 71% of the variation. The first axis (PC1) explained 42.4% while the second (PC2) explained 16.3% and the third (PC3) accounted for 13.2%. PC1 can be used to describe plant nutrient uptake efficiency, positively loaded by K, P and N_{leaf}. PC2 was positively loaded by SLA and negatively loaded by Mg (Figure 2.4a). PC3 largely explained physiological strategy, positively driven by P_N and negatively by $\delta^{13}C$ (Figure 2.4b). Overlaying site location onto the bi-plot demonstrated the variability in nutrient uptake and resource strategies among plantations. Trees at Montbeillard, Rapide-Danseur and La Motte were characterized by higher foliar nutrient uptake compared to the other two sites explained by PC1.

Trees at Rapide-Danseur demonstrated high rates of P_N while those at Montbeillard were characterized by higher ratios of $\delta^{13}C$ as seen in PC3.

2.4.3 Soil characteristics

Abiotic drivers of tree DBH, stand volume and survivorship

The main environmental drivers of mean tree DBH were interspecific competition from trees and shrubs, in addition to soil P, Ca, pH and percent of clay content (Table 2.4). Competitive influence from graminoid cover marginally explained mean tree DBH ($P = 0.08$). The relationship between DBH and soil pH was negative indicating that bigger trees were found on soils with slightly higher acidity. Conversely, a greater concentration of Ca was reflected by an increase in growth. High concentrations of clay negatively influenced tree growth, reducing mean DBH. Blocks containing the poorest growth at the site with the smallest mean tree DBH were largely composed of heavy clay (35-60%) (Figure 2.6). In contrast, soils at La Motte contained between 20-40% clay, which was reflected by increased tree productivity. The fixed effects accounted for 24% of the variance (marginal R^2) while the fixed and random terms combined accounted for 86% (conditional R^2).

Table 2.4 Linear mixed effect output explaining the fixed effects for diameter at breast height (DBH). The model estimate is present (E) with the standard error (SEM). The number of independent values associated with each model (d.f.) are presented as well as the probability of significance (*P*). Predictors included soil nutrients such as phosphorous (P), calcium (Ca), nitrogen (N), potassium (K), soil pH (pH), percent of clay soil, slope and percent vegetation cover (i.e. graminoid, herbaceous, shrub and tree).

Source of Variation	E	SEM	d.f.	*P*
P	0.26	0.12	148	0.02
Ca	0.57	0.13	93	<0.001
N	-0.86	0.75	155	0.25
K	-1.76	1.08	109	0.10
pH	-1.23	0.22	129	<0.001
Clay	-1.30	0.62	153	0.03
Slope	-0.005	0.02	153	0.82
Graminoid Cover	-2.50	1.44	140	0.08
Herbaceous Cover	-2.12	1.43	142	0.14
Shrub Cover	-4.19	1.45	140	0.004
Tree Cover	-9.45	2.79	153	<0.001

Note: Significant effect at $P \leq 0.05$.

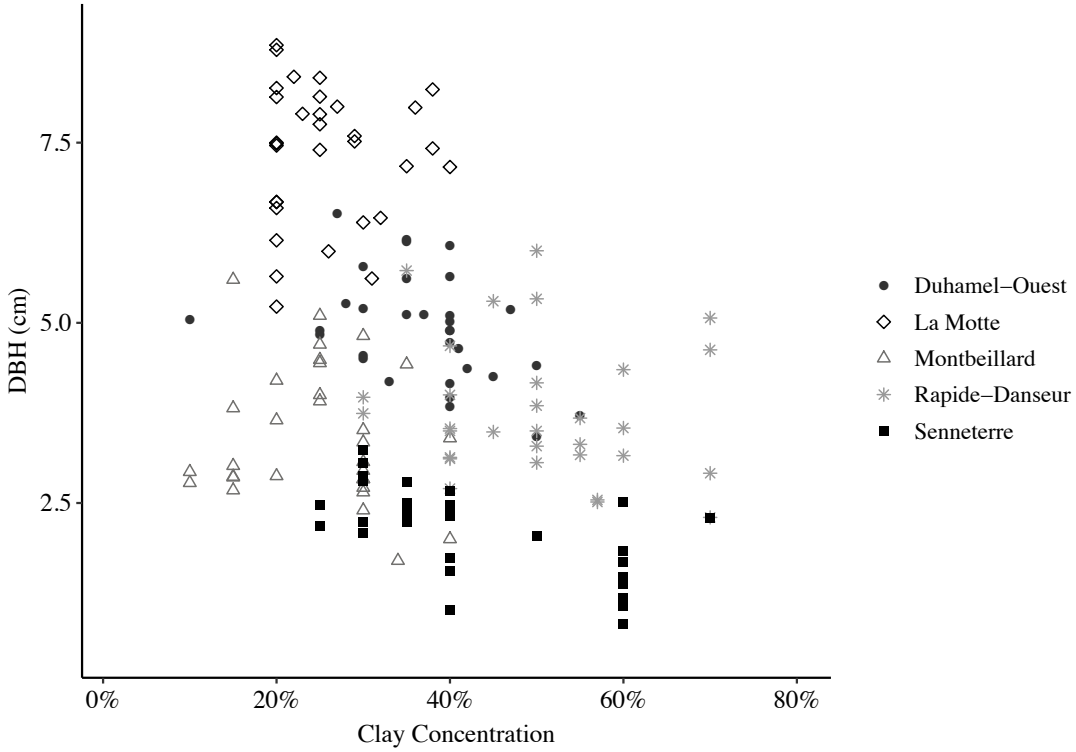

Figure 2.6 Relationship between mean tree diameter at breast height (DBH) and the proportion of clay in the soil. Each site is composed of eight provenances replicated across four blocks.

Similarly to mean tree DBH, stand volume was affected by Ca concentration, soil pH, clay content and the competitive influence from other trees and shrubs (Table 2.5). The presence of trees (i.e. *Larix*, *Populus* and *Picea*) and shrubs significantly reduced paper birch stand volume while the stands with high volume had increased soil concentrations of Ca and reduced percent clay content. The marginal R^2 for the model was 23% while the conditional R^2 was 87%. Similarly to stand volume the presence of other trees was also selected to characterize paper birch survivorship ($P = 0.01$). Increased interspecific competition from other trees had a significantly negative influence on paper birch survival resulting in higher paper birch mortality (Table 2.6). The marginal R^2 for the

model was 29% while the conditional R^2 was 41%. The large gap in variance explained by fixed and random terms in both the mean tree DBH and stand volume models indicates a stark degree of irregularity between sites, which in turn had a significant influence on the dependent variables. However, the conditional R^2 of the survivorship model suggests there are other factors influencing survivorship that were not accounted for.

Table 2.5 Linear mixed effect output explaining the fixed effects for paper birch stand volume. The model estimate is present (E) with the standard error of the mean (SEM). The number of independent values associated with each model (d.f.) are presented as well as the probability of significance (*P*). Predictors included soil nutrients such as phosphorous (P), calcium (Ca), nitrogen (N), potassium (K), soil pH (pH), percent of clay soil, slope and percent vegetation cover (i.e. graminoid, herbaceous, shrub and tree).

Source of Variation	E	SEM	d.f.	*P*
P	0.12	0.07	152	0.10
Ca	0.33	0.08	99	<0.001
N	-0.37	0.46	154	0.42
K	-0.43	0.68	124	0.52
pH	-0.71	0.14	138	<0.001
Clay	-1.28	0.38	154	0.001
Slope	-0.01	0.01	153	0.46
Graminoid Cover	-1.35	0.88	138	0.12
Herbaceous Cover	-1.34	0.87	140	0.12
Shrub Cover	-2.72	0.88	137	0.02
Tree Cover	-7.22	1.72	152	<0.001

Note: Significant effect at $P \leq 0.05$.

Table 2.6 Linear mixed effect output explaining the fixed effects for paper birch survival. The model estimate is present (E) with the standard error (SEM). The number of independent values associated with each model (d.f.) are presented as well as the probability of significance (*P*). Predictors included soil nutrients such as phosphorous (P), calcium (Ca), nitrogen (N), potassium (K), soil pH (pH), percent of clay soil, slope and percent vegetation cover (i.e. graminoid, herbaceous, shrub and tree).

Source of Variation	E	SEM	d.f.	P
P	-0.02	0.02	121	0.33
Ca	-0.02	0.02	42	0.37
N	0.009	0.17	110	0.95
K	-0.27	0.22	58	0.22
pH	-0.03	0.05	86	0.47
Clay	-0.002	0.14	128	0.98
Slope	0.002	0.006	132	0.70
Graminoid Cover	0.17	0.36	143	0.63
Herbaceous Cover	0.18	0.35	145	0.61
Shrub Cover	-0.38	0.36	143	0.28
Tree Cover	-1.49	0.66	141	0.02

Note: Significant effect at $P \leq 0.05$.

Relationship between abiotic variables in accordance to site

Four PCs were retained by the principal component analysis to investigate the relationship the edaphic characteristics between sites. The components cumulatively explained 81% of the variation in the traits investigated, with PC1 explaining 29.5%, PC2 explaining 23.4%, PC3 explaining 15.6% and PC4 explaining 12.6%. PC1 was negatively loaded with soil pH, Ca and percent of clay (Figure 2.7a). PC2 was negatively loaded with soil P and K, thus primarily explaining nutrient availability. PC3 was negatively loaded with shrub cover, while PC4 was negatively loaded with

tree cover (Figure 2.7b), cumulatively explaining interspecific competition at Montbeillard and Rapide-Danseur sites.

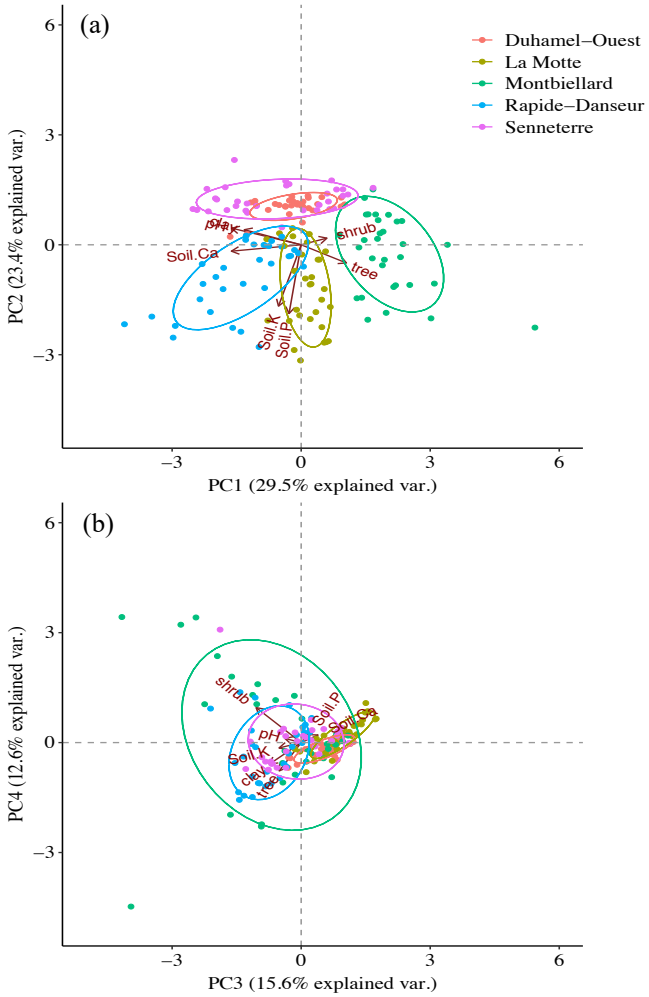

Figure 2.7 Principal component analysis dividing environmental variables into gradients that describe site characteristics. (a) PC1 plotted against PC2, where PC1 is driven by soil pH, Ca (Soil.Ca) and percent clay concentration (clay), while PC2 is driven by soil phosphorous (Soil.P) and potassium (K). (b) PC3 plotted against PC4, where PC3 is driven by percent shrub cover (shrub) and PC4 is driven by percent tree cover (tree).

2.4.4 Transfer function

Geographic and climate variables were not correlated to paper birch DBH or stand volume. Further, growth and survivorship responses in accordance to transfer distance were not statistically significant ($P > 0.05$; Table 2.7). This indicates that transferring provenances from seed origin to Abitibi-Temiscamingue did not impact the rate of growth or survivorship of the paper birch populations. Additionally, the climate of experimental plantations did not significantly impact the rate of provenance growth or influence survivorship at their respective sites ($P > 0.05$).

Table 2.7 Output from the quadratic transfer function of mean tree diameter at breast height (DBH), stand volume and survivorship. The model estimate is present (E) with the standard error (SEM). The marginal R^2 (R^2) are presented as well as the probability of significance (*P*). Climate and geographic predictors included elevation, latitude, mean annual temperature (MAT), maximum temperature during warmest month (MTWP), minimum temperature during the coldest month (MTCP), the annual temperature range (difference between the maximum temperature of the warmest period and minimum temperature of the coldest period; ATR), number of growing degree days above 5ºC (DD >5°C), mean summer precipitation (MSP) and mean annual precipitation (MAP).

	DBH (cm)				Stand Volume (m^3h^{-1})				Survivorship (%)			
Predictors	R^2	E	SEM	*P*	R^2	E	SEM	*P*	R^2	E	SEM	*P*
Elevation	<0.01	0.01	0.01	0.14	<0.01	0.02	0.02	0.43	0.07	-0.01	0.01	0.30
Latitude	0.02	0.13	0.75	0.86	<0.01	-5.19	31.54	0.87	0.10	0.21	0.15	0.18
MAT	<0.01	-0.003	0.007	0.62	<0.01	-0.01	0.01	0.47	0.16	-0.01	<0.001	0.08
MTWP	<0.01	0.01	0.01	0.21	<0.01	0.03	0.03	0.30	0.10	<0.001	<0.001	0.78
MTCP	<0.01	-0.02	0.01	0.09	<0.01	-0.05	0.03	0.12	0.13	-0.01	0.01	0.22
MAP	<0.01	<0.01	<0.01	0.61	<0.01	<0.01	<0.01	0.54	0.01	<0.001	<0.001	0.41
MSP	<0.01	-0.02	0.01	0.18	<0.01	-0.04	0.03	0.19	0.03	-0.01	0.01	0.43
DD>5°C	<0.01	<0.01	0.01	0.79	<0.01	<0.01	0.03	0.92	0.16	-0.01	0.01	0.32
ATR	<0.01	-0.08	0.04	0.06	<0.01	-0.04	0.02	0.12	0.08	<0.001	<0.001	0.92

Note: Significant effect at $P \leq 0.05$

2.5 Discussion

In this study, we evaluated the morphological and physiological differences amongst paper birch provenances, in addition to the environmental factors influencing their rapid growth and establishment on abandoned agricultural fields in northwestern Quebec. Our results revealed patterns of phenotypic plasticity within the physiological strategies and morphological traits of paper birch. Transferring provenances from differing ecoregions to a new climate did not impact their rate of growth or survival. In contrast to our hypothesis, model outputs demonstrated that relocating provenances from warmer to colder climates and vice versa had no effect on their productivity over 10 years of growth. Rather, differences related to growth and physiological strategy were largely attributed to site characteristics.

2.5.1 Physiological strategies and site influence

Although some resource strategies demonstrated difference between provenances, there was a high degree of variability within provenances. Further, such differences were small and did not provide a competitive advantage reflected by increased tree productivity. For instance, southern provenances with higher SLA compared to those found along a mid-latitudinal gradient were not reflected by an increase in photosynthetic rate or growth pointing to adaption via phenotypic plasticity. Previous studies found that provenances located in environments with increased rates of precipitation resulted in leaves with higher SLA and photosynthetic rates (Chapin and Eviner, 2005). In addition, southern provenances have longer growing seasons, potentially providing a competitive advantage (Hawkins and Dhar, 2012). Thus, we hypothesized that provenances of southern origin would outperform northern or local provenances, however, our results contradicted this. Provenances had similar punctual photosynthetic rates, reflected by similar mean tree DBH and stand volume. Although

we did not capture leaf senescence to calculate the length of each provenance growing season such differences were not reflected by increased productivity. Therefore, if such differences existed, it is unlikely they were drastic in comparison or provided any type of competitive advantage.

Nutrient availability varied significantly across sites, however, provenances had similar macro-nutrient uptake, with the exception of K. In order to grow and survive, plants require a combination of macro and micro nutrients, yet the degree of their availability can depend on soil characteristics (Marschner and Rengel, 2012). The most productive site, La Motte, had similar concentrations of foliar P in comparison to the moderately productive sites, Montbeillard and Rapide Danseur, in addition to significantly higher concentrations of N_{leaf} than Montbeillard. Conversely, concentrations of N and P were significantly lower in the leaves and soil at the second most productive site, Duhamel-Ouest. Being the most recently abandoned agricultural field, farming practices are likely the cause of such nutrient depletion. Such findings demonstrate the ability of paper birch to maintain productivity in the presence of low N and P, an important implication for Abitibi-Temiscamingue as clay soil often reduces the amount of soluble phosphates available for plant uptake due an increased rate of fixation (Gerard, 2016). Similar P uptake was observed in the leaves of provenances at the least productive site and yet tree growth was drastically impeded, indicating trees were not limited by P availability. Rather, trees exhibited signs of stress due to soil texture. The site was characterized by poor nutrient availability, low concentrations of ^{13}C, low rates of photosynthesis and high clay concentrations. Research indicates compact clays restrict drainage capability, increasing the risk of waterlogged soil, which can result in stunted tree growth (Russel, 2002). Our study suggests there is an optimal ratio of clay to increase paper birch productivity. Soil at the most productive site was slightly acidic, nutrient rich and composed of 20-40% clay. In contrast, the site with the poorest growth was mainly composed of heavy clay, containing up to 70%. Water availability was not a factor of concern evidenced by the relatively low $\delta^{13}C$ values and relatively large SLA for this site. Although, not covering a significant portion of area, there was an

abundance of shrubs and *Larix* present indicating the presence of a high moisture regime. Low rates of P_N suggest the high concentration of clay and abundance of water could be negatively impacting tree growth. The high retention of water and poor drainage in clay soils can displace oxygen and reduce respiration in roots (Kelting et al., 1998). Consequently, plants that produce inadequate levels of ATP, supress important mechanisms such as protein synthesis and close stomates leading to the inhibition of photosynthesis (Parent et al., 2008).

Although Ca increases phosphate fixation, it is required for plant growth and plays a role in increasing the porosity of clay soil (Gerard, 2016; Wuddivira and Camps-Roach, 2007). Studies have found increased concentrations of Ca can improve the friability of the soil by breaking up clay particles (Muneer and Oades, 1989). Our results corroborate such findings as sites composed of heavy clay and Ca reflected higher rates of growth than those with increased clay content and low levels of the macronutrient. Thus, areas in Abitibi-Temiscamingue composed of heavy compact clay soil are less suitable for paper birch plantations as they increase the risk of hypoxia and restrict the ability of roots to penetrate soil (Gerard et al., 1972).

Our study demonstrated how provenance water strategies changed based on the site location. Water use seemed to vary significantly between Senneterre and Montbeillard with populations displaying evidence of drought stress in the later. Provenances exhibiting signs of drought stress were found at a site generally characterized by low clay concentrations. In contrast to clay soil, sand particles are large and porous with low water retention capability (Rawls and Brakensiek, 1982). Thus, sites demonstrating limited water availability reflect increased leaf $\delta^{13}C$ values of provenances with poor water use strategies and reduced growth. Provenance strategy at this particular site appears to reflect local adaption to a small degree as southern populations experienced drought stress in comparison to local northern provenances, which exhibited efficient water use strategies. However, this trend could not be established across all sites exemplifying the significant role phenotypic plasticity plays in the expression of certain

phenotypes as a response to heterogenous environmental conditions. Similar adaptive patterns have been documented in European beech, where provenances exhibited a higher degree of phenotypic plasticity rather than local adaption in a common garden experiment with site strongly influencing growth (Müller et al., 2020).

Our study revealed that paper birch growth and stand volume were negatively impacted by competitive influence from trees, including those belong to the genera of *Larix*, *Picea* and *Populus*, in addition to shrubs such as *Salix* and *Alnus*. Further, low survivorship was recorded on sites with increased canopy cover from other tree species. Sites exhibiting limited water and nutrient availability appeared to have the highest degree of competition resulting in lower survivorship and reduced growth. The findings from our study indicate some degree of vegetative control may be required in plantations to optimize paper birch productivity and reduce competitive influence for space and resources.

Stand volume was impacted by tree mortality with some sites having reduced yields even in the presence of trees with higher individual volume. Survivorship data was not recorded over the duration of the plantation's development, thus it is difficult to estimate the specific drivers of survivorship. Our study acknowledges the negative competitive influence of other tree species on birch survivorship, however, mortality likely occurred in the early stages of growth. Montbeillard, a site with lower survivorship, was ploughed and harrowed in the spring. Generally these procedures are done before winter to help reduce compaction within the soil. Thus, soil conditions at the time of planting may have increased the rate of mortality at this particular site. Further, low survivorship may have arisen due to improper planting or handling techniques and herbivory during the initial stages of paper birch establishment. Further, tree mortality was not frequently recorded among mature stands concluding that low survivorship occurred during juvenility.

2.5.2 Conclusion

The high phenotypic plasticity observed among provenances aids in the ability of paper birch to adapt to changing climate conditions across Abitibi-Temiscamingue. The flexibility exhibited by traits make this species suitable for intensive management as it can withstand various environments. With large portions of abandoned farmland scattered across the region and the economic value of birch fibre, establishing paper birch plantations could increase the profit margins of private and public forest sectors, while maintaining sustainable forestry practices. Planting populations in areas of high quality is imperative for optimal paper birch growth and survival. Specifically, areas composed of moderate clay, slightly acidic soil and low interspecific competition are suitable for plantation. P fertilization can be used to reduce the nutrient deficiency of an area, thereby increasing productivity while promoting growth in plantations. However, our results indicate that in areas of compact clay, fertilization may not be as effective as heavy clay plays a more significant role by reducing root distribution and increasing the risk of waterlogged soil. Although our study provided strong evidence of adaption via phenotypic plasticity, it is not to say that genetic assimilation does not exist among paper birch populations across greater latitudinal gradients as our work focussed on terrestrial populations across Quebec.

2.6 Acknowledgements

This study was funded by Canadian National Science and Engineering Research Council (NSERC) through project 476504-2014. Special thanks to Dr. Francine Tremblay for spearheading the initial stages and contributing to the development of the project. We appreciate the help of Michel Guimond and Eva Thévenin during the collection of field data. We thank Jian Wang and Barb Thomas for their input regarding study design. We acknowledge the support provided by Syndicat des Producteurs de

Bois d'Abitibi-Témiscamingue (SPBAT) and the stakeholders who provided their land for our research endeavours.

CHAPTER III

GENERAL DISCUSSION

The goal of our research was to fill in some of the knowledge gaps surrounding the natural variability of paper birch traits and their physiological strategies. More specifically, we aimed to investigate how the genetic variability of this species influences growth and establishment across Abitibi-Temiscamingue. Further, understanding the influence of adaption strategies provides useful insight for future tree improvement programs, which can increase the productivity and economic profit of paper birch.

Our study indicated paper birch productivity was largely effected by heavy clay soil. Stunted tree growth was observed at a site characterized by heavy clay soil and the lowest punctual P_N. Additionally, increased rates of mortality and reduced resource availabilty were observed at plantations with high interspecific competition, reducing paper birch growth and establishment. Conversely, plantations with slightly acidic loamy soil and low competitive influnece exhibited optimal rates of productivity. After being translocated, provenances were not effected by changes in climate. Further, provenance physiological strategies were largely dependent or influenced by site characteristics. Such findings allude to adaption via phenotypic plasiticy. Our research provides promising outcomes for the Quebec forestry industry as it demonstrates how paper birch from various inland ecoregions can be transplanted across the province. However, our study was limited in the types of populations that could be collected. It is possible that our results point solely to phenotypic plasticity because there was not enough climatic difference between Quebec eco-zones. Thus, further research needs to

be conducted to capture the genetic influence of paper birch across a wider geographic distribution to determine whether local adaption plays a role in growth strategies across provinces. Such knowledge would be useful for forestry industries and private stakeholders across Canada.

3.1 Factors influencing tree productivity and survivorship

Given the plastic nature of paper birch traits, translocating provenances to a new climate did not impact their rate of growth or survivorship as populations acclimatized to the new conditions. Rather than climate, paper birch productivity was impeded by high concentrations of clay. Our results outlined the importance of balanced clay content within the soil. Heavy clay can stunt tree growth as a result of lower P availability (Gerard, 2016), waterlogged soil and the restriction of root development (Russell, 2002). Further, agricultural research has well documented the impact of compact clay restricting root growth and morphology resulting in yield reduction (Chen et al., 2005; Schumacher and Smucker, 1981). However, the low water retention capability of sand particles may increase the risk of drought stress as observed in our study. Thus, moderate concentrations of clay were beneficial to growth. In addition, clay influences nutrient availability (Kome et al., 2019). While abundant with important mineral nutrients (Ristori, 1979), high clay ratios reduce available phosphates for plant uptake (Gerard, 2016) negatively impacting soil fertility.

Soil water and nutrient availability are some of the first features tested when quantifying site potential. However, soil pH can significantly impact on the productivity of a given site. Research has determined the most optimal soil pH ranges from 6.5 to 7.5 as most plant nutrients are readily available for resource extraction (McCauley et al., 2009). Alkaline soils generally have lower concentrations of micronutrients, while acidic soils are considered optimal due to their increased availability (McCauley et al., 2009). Both acidic and alkaline soils increase the rate of phosphate fixation (Binkley and Vitousek, 1989). At a slightly lower pH phosphate

ions react with iron and aluminum, creating compounds that are insoluble and not available for plant uptake (Binkley and Vitousek, 1989). Similarly, soil pH above 7.5 creates an environment where phosphates bind to calcium and magnesium to form compounds difficult for plants to absorb (Binkley and Vitousek, 1989). Our findings suggest that paper birch is well equipped to succeed on acidic soils. All sites were located on slightly acidic soil with means ranging from 5.8 to 6.4. However, the site with the highest degree of productivity and strong survivorship had less variability in the soil pH, averaging at 5.85. The plantation with the poorest growth ranged from 5.5-6.91 with an average pH of 6.29. Based on the literature, soil microbial activity appears to operate most effectively in slightly acidic soils (Pietri and Brookes, 2008). Microbes are essential for fertile soils as they decompose organic matter reducing the substance to a usable form to plants (Miransari, 2013). Thus, soil pH may have influenced tree growth, however, we theorize soil texture was the main driver of productivity and establishment in our plantations. More importantly, our study corroborates knowledge regarding the ability of paper birch to tolerate a wide range of soil physical and chemical properties, including acidic soils.

Species living in the same space competing for the same resources is known as interspecific competition and can have adverse impacts on plant fitness (Craine and Dybzinski, 2013). Our findings suggested that paper birch productivity decreased as a result of competition from neighbouring shrubs and trees, while mortality increased as a result of interspecific competition from other trees. Shrubs are known competitors for nutrients and root distribution (Zhang et al., 2006) with studies identifying a relationship between high shrub density and the growth reduction of conifer stands (Cortini and Comeau, 2008). In order to compete with neighbouring plant communities, trees have developed various strategies to acquire nutrients, space and light (Metz et al., 2013; Bolte and Villanueva, 2006; Aerts, 1999). The reduction in growth, stand volume and survival observed at the most competitive site suggests that shrubs or spruce were more effective competitors. Traditionally pesticides have been used to control aggressive species, however, as of 2001 Quebec suspended the use of

chemical herbicides as a measure of the “Stratégie de protection des forêts” (Thiffault and Roy, 2011). Our results demonstrate the need for more intense management of competitive species.

3.2 Study limitations

Physiological strategies such as gas exchange, require measurements to be taken before stomates close due to heat stress (Peìrez-Harguindeguy et al., 2013). Thus, we were confined in the number of trees that could be measured as a result of time constrictions and limited battery power in the field. In addition, only one gas exchange measurement could be recorded for each provenance at each site due to logistics. Having additional measurements may have provided a more accurate account of provenance photosynthetic rate.

The scope of our research was to investigate the adaption strategies of paper birch in Quebec, however, we were restricted to provenances from inland locations and therefore, lacked contrasting environmental zones like the coast. Thus, our results show promising implications for the forestry industry within the province but are confined in their ability to demonstrate the genetic variabilitly that exists within paper birch. We were unable to measure populations with vastly different climates, such as those found along the coast or provenances from other provinces, which could have presented greater evidence of local adaption.

3.3 Ecological significance

Our research highlighted the retained ability of paper birch functional traits to be plastic. Recent studies have largely focussed on expression and the evolutionary function of phenotypic plasticity (Bakhtiari et al., 2019). Here we examine the role of plastic traits and their ability to influence physiological strategies and impact tree

productivity after translocation. Our results demonstrated the ability of paper birch phenotypes to exhibit various expressions as a function of differing environmental conditions. Not only does this demonstrate the suitability of all terrestrial paper birch provenances to be used in intensively managed plantations across Abitibi-Temiscamingue but it stimulates discussion surrounding climate change. After being translocated to a foreign climate, provenances from differing eco-regions adapted to new abiotic influences. Climate change is rapidly altering environmental conditions around the world (McNutt, 2013). Regional climate models of Ontario and Quebec have projected increases in seasonal temperatures (Kharin et al., 2007). This may present challenges to species well adapted to the harsh and cold climate of Abitibi-Temiscamingue. However, our research provides insight regarding the ability of paper birch to adapt and alter resource acquisition strategies based on environmental influence. Thus, in addition to the quality of wood fibre, the plastic nature of paper birch traits increases the economic profitability of the species.

3.4 Implications for sustainable forestry management

Paper birch is a fast growing, hardwood species that can be harvested after 55-65 years of growth (Safford et al., 1990). In addition to a relatively large and plastic gene pool (Hawkins and Dhar, 2012), such characteristics make paper birch a suitable species for hybridization and intensive management. Further, our results revealed that the early successional species performs well on abandoned agricultural fields. One of our sites was recently deserted (>15 years) and exhibited low levels of N and P within the soil, likely as a result of previous farming practices. Although sites reflected differences in the uptake of important nutrients in birch leaves, this site did not exhibit evidence of stunted growth. Rather, provenances displayed the second highest mean tree DBH. Thus, due to the plastic nature of birch traits, abandoned farmland can be turned into a profit to benefit the public and private forestry sectors, with considerations regarding suitable soil textures.

There was a large degree of variation within and among provenance resource strategies. Where provenance related differences occurred, they were found to be small and did not provide a competitive advantage over other populations. Thus, local populations did not outperform those translocated from various ecoregions. This provides immense knowledge regarding the capability of outsourced paper birch populations and their ability to adapt to new environments. Such knowledge can be useful for future hybridization and tree improvement programs in the region.

As an early successional species paper birch can establish itself in areas not tolerated by other species and ameliorate soil conditions by returning essential nutrients to the soil in the form of leaf litter (Simard, 1996). Paper birch has a wide distribution and can withstand various climate and edaphic regimes. Typically, paper birch prefer environments composed of loamy, well drained, moist and acidic soil (Safford et al., 1990). Additionally, birches have adapted to grow in cool climates (Safford et al., 1990). Paper birch has been known to quickly establish itself and dominate resource rich soils, however, the species can readily pioneer unfavorable soil conditions in addition to clay and sandy soils (Safford, 1983). Some studies have highlighted the inability of paper birch root systems to penetrate certain depths in clay soils, providing challenges when trying to achieve optimal growth in a clay based environment (Gerard et al., 1972). Located along the clay belt, Abitbi-Temiscamingue is largely composed of clay deposits remnant of the Barlow and Ojibway proglacial lakes (Bergeron et al., 2007; Bergeron et al., 1986). The region is highly susceptible to soil rutting and compaction due to the heavy composition of clay and organic matter content, in addition to the historical use of the land (Lefort et al., 2002). However, various techniques can be used to alleviate poor soil conditions. Although heavy clay soils increase the rate of phosphate fixation leading to a general depletion of phosphate ions readily available for plant uptake, recent studies demonstrate how the fertilization of plantations with P can help stimulate the growth and establishment of hardwood trees (Guillemette and DesRochers, 2008). Mechanical methods such as ploughing and discing reduce compaction by loosening the soil, in turn increasing aeration

(DesRochers and Tremblay, 2009). Further, mounding techniques have been proven to improve soil drainage and aid in the management of weeds (DesRochers and Sigouin, 2014).

Over the initial 10 years of growth, weed management was limited to allow the facilitation of understory vegetation. However, our research indicates that rigorous management of tree and shrub species is required to suppress or eliminate undesirable vegetation, thereby promoting birch growth and establishment. Low resource environments resulted in strong interspecific competition from species such as *Alnus*, *Larix*, *Picea* and *Salix*, reducing birch productivity. Thus, to increase the availability of important resources total or partial weed removal should be implemented in birch plantations. Although chemical treatments are effective and financially feasible, the suspension of herbicide use in Quebec (Roy et al., 2003) limits management techniques to physical efforts. The suppression of certain species can be achieved by cutting weeds back or flush along the surface of the ground. Albeit more extensive, species can be eliminated by cultivating the plant entirely. Overall, it is imperative to monitor and reduce the development of competitive plants over the duration of the plantation by removing them when they are young.

3.5 Future research

Our findings touch on the importance of site quality and how heavy clay may influence stunted growth among tree populations. In the presence of low macro-nutrient availability and aerated soil, birch trees were able to maintain productivity. Therefore, the fixation of P in clays may not be as big of an influence on growth or establishment as compact soils. Additionally, soils saturated with water over an extended period of time can impede growth by inducing stomatal closure, leaf senescence and root decay (Russel, 2002). Previous studies outline the sensitivity of paper birch roots in clay soils (Perala and Alm, 1990) as their thin root systems (Dufresne et al., 2011) have difficulty penetrating through the soil (Perala and Alm, 1990). This leads to the question of

whether soil compaction or water retention plays a bigger role in stunted tree growth. Given the high concentration of clay soil across Abitibi-Temiscamingue, further research is required to understand how soil texture specifically impacts the physiological structure of paper birch root systems.

Paper birch provenances did not reflect differences in productivity, however, further research should be conducted to investigate the timing of bud break and susceptibility to infestation. Bud burst and growing season length are crucial for assessing a species' susceptibility to spring frost damage, infestation, survivorship and overall growth after populations have been transplanted (Li et al., 2003; Hawkins and Dhar, 2012; Pyakurel and Wang, 2014). A bud phonological study by Simpson et al. (1999) indicated that bud development has a genetic basis. Additional studies concluded that bud break follows a latitudinal trend from south to north further supporting the concept of genetic control (Simpson et al., 1999; Cooke et al., 2012; Hawkins and Dhar, 2012; Basler and Körner, 2014). However, it still remains unclear to what extent environmental factors such as temperature and water availability influence growth differences amongst paper birch provenances, in regards to bud development, over the course of a growing season in a common garden experiment. In the field we observed a general pattern with some of the southern provenances breaking bud earlier and losing leaves later in comparison to other more northern provenances. Although climate variables had no significant effect on provenance growth, earlier bud break and late senescence could increase their vulnerability to infestation and frost damage. Thus, more research is required to investigate whether the timing of bud burst and growing season length, after translocation, makes provenances more susceptible to high rates of infestation.

Lastly, the research conducted in this study should be used to continue investigating the influence of interspecific competition. Our research highlighted the negative effects of competition from the presence of neighbouring plant communities in resource deficient environments, however, more research is needed to quantify how this impacts paper birch morphology. It has been established that plants compete for light, nutrients,

water and space. Therefore, in a competitive environment are the roots or canopy structure of paper birch restricted or modified in various ways? The knowledge acquired from containing this work could further aid in the management of competitive interactions within plantations.

APPENDIX

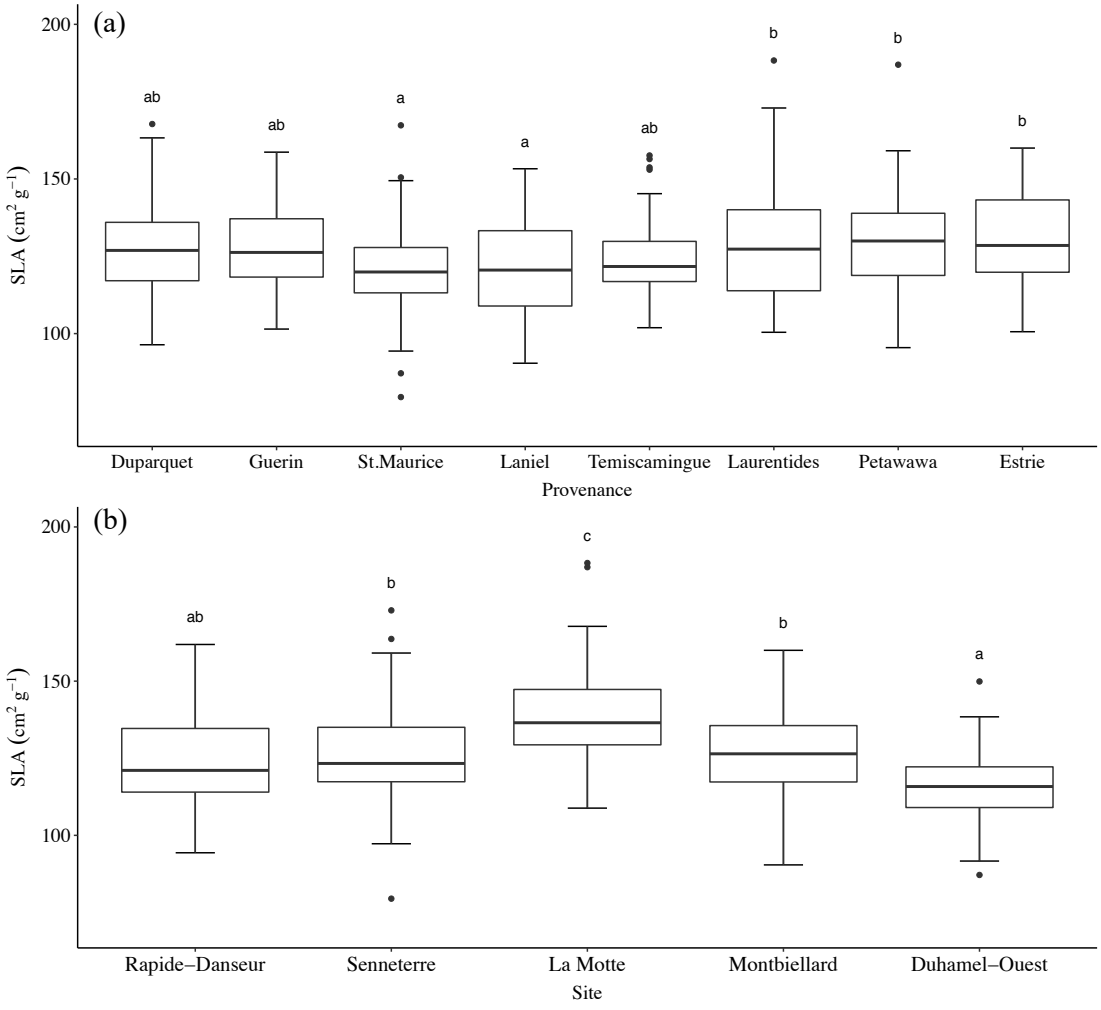

Figure 1. Mean specific leaf area (SLA) with significant differences between (a) provenances and (b) site locations. Means with different letters are significantly different at $p < 0.05$. The standard error is present for each provenance and site value.

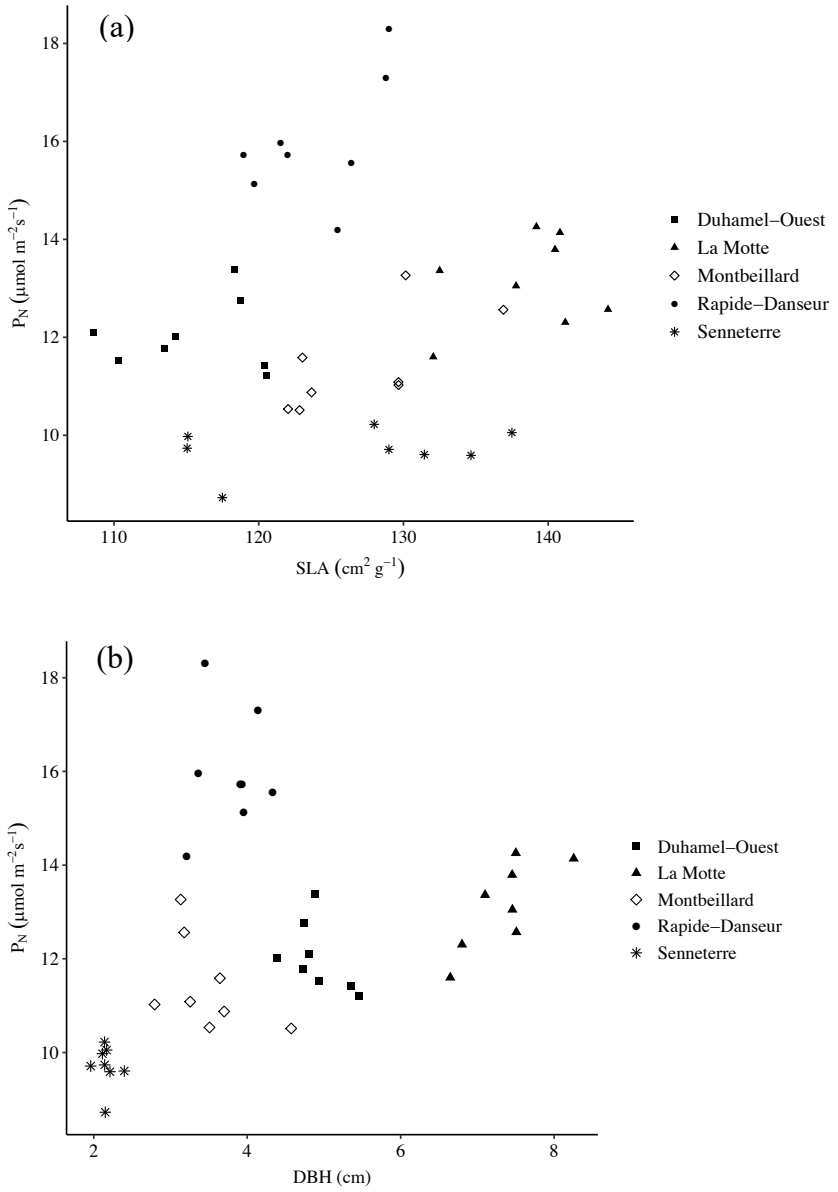

Figure 2. Mean provenance values of leaf net photosynthetic rate (P_N) plotted against (a) specific leaf area (SLA) and (b) mean tree diameter at breast height (DBH) across each site. Rapide-Danseur displays significant differences in P_N compared to Senneterre, Montbiellard and Duhamel-Ouest. La Motte significantly differed from Senneterre.

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